Implications of climate change on the reproductive success of the Southern Yellow-billed Hornbill, *Tockus leucomelas*

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ABSTRACT

The effects of environmental warming on the reproductive performance of birds are most easily studied in desert habitats where birds already experience air temperatures (T_as) close to their upper thermal tolerance. Many desert birds coincide breeding with periods of food availability triggered by rainfall during the summer season. Daily maximum air temperatures (T_{max}) during the Kalahari summer season frequently reach the lower forties (°C) and recent years have been characterised by reduced rainfall and increased T_a. Breeding Southern Yellow-billed Hornbills (*Tockus leucomelas*) could be particularly vulnerable to high T_a due to their breeding strategy whereby the females are confined to the nest cavity for most of the nesting period. During this time their male partners are solely responsible for food provisioning, which imposes a considerable energetic demand. In this thesis, I investigated the extent to which T_a affects the ability and willingness of breeding males to provision their female partners and offspring. And consequently, the extent to which male investment and the thermal environment affect female body mass (M_b) and chick development rates in Southern Yellow-billed Hornbills in the Kalahari.

During three consecutive hornbill breeding seasons (October – March, between 2012 and 2015), I collected life history data during 50 breeding attempts by 32 hornbill pairs. At the study site, Southern Yellow-billed Hornbills readily breed in artificial nest boxes and this allowed me to assess the internal nest climate using temperature and relative humidity loggers which were placed in most of the nests. The male hornbills in the study population were semi-habituated which facilitated behavioural observations. Weather data were recorded at an on-site weather station. Morphometric data from females and chicks were collected on a daily basis at selected nests and perch scales installed at nest entrances recorded M_b data of the provisioning males. From chick hatching to chick fledging, I observed the behaviour of the males during 30-min focal follows and focussed on foraging behaviour, prey allocation decisions (nest versus self), microsite use and thermoregulatory behaviour.

Male hornbills spent more than half of their time panting at T_as above 34.5 °C. Days on which this threshold temperature was exceeded were therefore described as ‘hot days’. The male hornbills experienced trade-offs on hot days between foraging efficiency and panting behaviour, indicating that the additional cost of thermoregulation and high T_a affected foraging success (Chapter 2). Males would always provision larger prey items to the nest and consumed the smaller prey items themselves. As T_a increased, the males increased their foraging effort,

but caught fewer and smaller prey items overall, reducing the total biomass they provisioned to the nest as well as the biomass they consumed. As a result, males were unable to maintain their M_b on days when T_a exceeded 37.9 °C (Chapter 3). A similar effect of hot days on M_b maintenance was observed in females and chicks within the nest. Independent of chick age, females departed the nest when their M_b reached a lower limit of 189.3 ± SD 18.1 g. The females would then aid the males in nest provisioning, however the negative effect of increasing T_{max} on provisioning rate was still evident; i.e. females were not able to compensate for reduced male provisioning rates on hot days. High T_as during the nesting period resulted in smaller and lighter fledglings and overall reduced the probability of a successful nesting attempt (Chapter 4). A thermal imaging experiment revealed that the large beak of hornbills (both males and females) plays an important role in non-evaporative heat loss. Hornbills were observed to dissipate up to 19.9 % of the total non-evaporative body heat loss via the beak. This water-saving mechanism can be highly advantageous to hornbills living in arid regions where water availability is limited (Chapter 5). Lastly, a comparison of the results of the current study with those of a study on the same hornbill population carried out between 2008 and 2011 revealed that mean T_{max} as well as rainfall during the nesting period had an important impact on overall hornbill reproductive effort and success (Chapter 6).

Long-lived species are expected to prioritise future reproductive opportunities over current broods. However, the predicted scenario for the Kalahari is that high T_as become more extreme and periods of drought become more frequent. Therefore, I predict an increased risk of breeding failure among Southern Yellow-billed Hornbills in the future which could affect the persistence of this population.

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Finishing this PhD thesis has left me with a great feeling of fulfilment, but also a little bit of sadness. I thoroughly enjoyed every aspect of this project and gladly accepted the opportunity to add a third field season to expand my dataset. Now that it has come to an end, I am going to miss it and I feel there are some unanswered questions that I would have liked to investigate further. There are many people who provided support during my PhD and I hope I haven't forgotten anyone; you have all been great!

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DECLARATION

This thesis reports original research that I conducted under the auspices of the Percy FitzPatrick Institute, University of Cape Town. All assistance received has been fully acknowledged. This work has not been submitted in any form for a degree at another university.

Signed: 

Date: 10 March 2017

PAPERS ARISING FROM THIS THESIS

van de Ven, T. M. F. N., R. O. Martin, T. J. F. Vink, A. E. McKechnie, and S. J. Cunningham. 2016. Regulation of Heat Exchange across the Hornbill Beak: Functional Similarities with Toucans? PLoS ONE 11: e0154768

The data published in the abovementioned paper are presented in Chapter 5 of this thesis. The chapter additionally includes an extended discussion on the relevance of the heat exchange mechanism to breeding hornbills. My input towards the publication of this paper was the greatest and included the construction of the equipment, study design, execution of data collection in the field, analysis of the data, the drafting of the manuscript and responding to the reviewers. R.O. Martin provided the idea of the study and assisted in data analysis. T.J.F. Vink assisted in the data analysis and the graphical presentation of the results. A.E. McKechnie was my co-supervisor and assisted in the experimental design, gave guidance in the field and assisted in the analysis. S.J. Cunningham was my supervisor and was therefore involved in all aspects of the study providing extensive advice and guidance. All co-authors provided comments to multiple versions of the manuscript.

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CHAPTER 1 INTRODUCTION

1.1 Climate change and arid ecosystems

The latest report of the Intergovernmental Panel on Climate Change (IPCC, 2014) addresses changes in extreme weather and climate events and concludes that climate extremes may result from a combination of i) a shift in air temperature (T_a; see list of abbreviations) distribution towards a warmer climate, ii) an increase in T_a variability, or iii) a changed symmetry from the norm of the temperature distribution towards the hotter part of the distribution. Climate change is being manifested as a higher frequency of occurrence and more intense heat waves, droughts and floods (Easterling et al., 2000). Recent climatological research in South Africa confirms a pattern of increasingly warm weather with an increase in the frequency of very hot days (Kruger and Shongwe, 2004; Kruger and Sekele, 2012; van Wilgen et al., 2016). Particularly strong warming trends have been identified in the Western and Northern Cape Provinces of the country where habitats are semi-arid and precipitation is highly variable (Kruger and Sekele, 2012). Especially in the past 15 years, the number of very hot days per year (T_a > 40 °C) has increased in the southern Kalahari region (Figure 1). Arid ecosystems are particularly sensitive to variability in weather fluxes, because of the close relationship between weather and biological activities in those systems (Huxman et al., 2004). For example, vegetation cover in desert ecosystems, like the Kalahari, is highly correlated with summer rainfall and in times of drought a low vegetation biomass impacts trophic structures and biodiversity, and potentially the mobility of sand dunes (Porporato et al., 2003; Nash and Endfield, 2007). In addition, high T_as impact the physiological functions of animals, for example in endotherms these can eventually lead to dehydration, hypocapnia and respiratory alkalosis (Dawson, 1982). Increased occurrences of prolonged periods of abnormally hot weather (heat waves) and droughts due to climate change are therefore expected to impact biological communities in arid ecosystems globally.

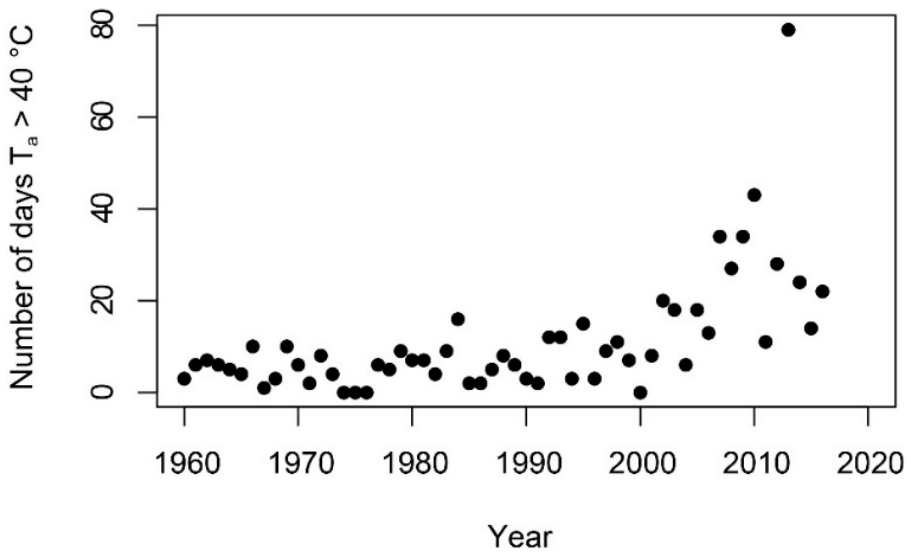

Figure 1 Number of days per year that daily T_a exceeded 40 °C, from 1960 to March 2016. Data were obtained from the weather station at Twee Rivieren, Northern Cape, South Africa (~ 120 km from the study site), South African Weather Service, SAWS.

1.2 Species' vulnerability to climate change

Species have been observed to respond to changing environments by changing their distribution ranges and phenology, resulting in shifts in community composition and ecosystem dynamics (Walther et al., 2002; Parmesan, 2006; Franklin and Seebacher, 2009). Genetic adaptation and phenotypic plasticity of organisms to changes in the environment have also been predicted for the future (Fuller et al., 2010). Climate change is occurring rapidly and some species are unable to adapt at this rate as is evidenced by population declines and increased risk of species extinctions (Parmesan, 2006; Bellard et al., 2012). Constraints on adaptation to climate change may be exacerbated by increases in the frequency of temperature anomalies rather than absolute temperatures (Jiguet et al., 2006). Heat waves are occurring more frequently as the climate changes (Albright et al., 2011) and occasional avian mass mortalities in response to extreme heat events confirm that the physiological capacity of birds, and potentially all endotherms, to offload heat in response to extreme high T_as can be overwhelmed (Welbergen et al., 2008; McKechnie and Wolf, 2010). Impacts of climate change affect species in different ways, which intensifies the need to identify vulnerability and resilience among species in order to direct conservation efforts (Şekercioğlu et al., 2012).

As outlined by Dawson et al. (2011), species' vulnerability to climate change can be evaluated by i) the extent of exposure of the species to climate events; ii) the sensitivity of a species to its environment; and iii) the capacity of a species to adapt to a changing environment. The degree of exposure of a species to the effects of climate change is species specific and

dependent on the variability of the regional weather events and changes in habitat structure. Through behavioural adjustments, animals can reduce their exposure by selecting sheltered microsites (i.e. burrows, cavities or foliage cover) (Wolf and Walsberg, 1996). Conversely, animals may experience increased exposure as a result of habitat destruction and fragmentation (Hof et al., 2011). Sensitivity is determined by the physiological and behavioural capacities of individuals of a species to respond to environmental changes (Portner and Farrell, 2008). The capacity of species to respond (resilience) to a changing environment depends on species-specific traits like thermal tolerances and the degree of genetic diversity within the population (Huntley, 2007; Williams et al., 2008). Identification of the resilience and sensitivity of species to warming environments highlights which species are already vulnerable or will become vulnerable in the near future.

Multiple studies have used climate envelope models in an attempt to predict the persistence and future ranges of species in the face of climate change (Buckland et al., 1996; Venier et al., 1999; Harrison et al., 2003). Climate envelope models are based on future predictions of climate change and current species' climate tolerances, and assume that the subset of climatic conditions a species currently occupies is an accurate predictor of its future distribution. However, climate envelope models do not take into account changes in habitat availability or possible capabilities of species to adapt or adjust to temperature and precipitation changes (Helmuth et al., 2005; Helmuth, 2009; Smit et al., 2016). A more empirical, albeit less predictive, approach to the question of adaptability is to directly record species' capacities to persist during extreme weather events, such as heat waves (Jiguet et al., 2006). Huntley et al. (2010) propose the use of dynamic models based on sensitivity analyses (i.e. population demographics, potential for dispersal and ecological processes), which can identify the factors that limit species' abilities to respond to climate change. Single-species studies can improve understanding of the physiological and behavioural mechanisms by which climatic variables affect species, providing valuable information that can aid in the construction of management plans (Foden et al., 2013). Mechanistic models combine ecological and physiological data and are useful to predict animals' responses to habitat and climate changes, for example increases in T_a (Kearney and Porter, 2009). Such an approach requires an adequate sampling effort of multiple variables that are hypothesised to affect a species' capacity to persist. In order to understand how intermediate processes are affected by high T_as, the current study modelled physiological and behavioural responses of a bird species to a range of T_as.

1.3 Limitations to physiological and behavioural adjustments to climate warming

In endotherms occupying hot environments, heat gain through metabolic activity and the environment must be balanced by heat loss at the same rate in order to maintain a constant body temperature (T_b). Environmental conditions that fall below or above the thermoneutral zone of an endothermic organism (a temperature range across which energy expenditure for the maintenance of stable T_b is minimised), will by definition lead to increased energy expenditure and water-loss (Withers, 1992; Schmidt-Nielsen, 1997; Williams and Tieleman, 2001). For this reason endotherms inhabiting extreme environments, such as deserts, have received much attention in studies of ecological energetics (Root, 1988; Weathers and Sullivan, 1993).

Factors influencing energetic costs related to thermoregulation include metabolic heat production, conductive and convective heat exchange, radiative heat exchange, evaporative heat loss and storage of heat via facultative hyperthermia (Schmidt-Nielsen, 1997). Desert-dwelling species can elevate their T_b in response to high T_as, but are physiologically restricted (by biochemical and tissue functioning) in the extent to which they can adapt by increasing set-point T_b in response to increases in T_a (Marder et al., 1989; Mongold et al., 1996; Smith et al., 2000; Boyles et al., 2011). In water-scarce environments, the need to conserve water is often in conflict with the need to evaporate water in order to regulate T_b (Webster, 1991); this trade-off between hyperthermia and dehydration avoidance is a fundamental aspect of a desert existence.

Sedentary species residing in deserts have evolved under continuous exposure to extreme T_a, both low and high, and should have a high resilience to extreme T_a (Maclean, 1984; Gardali et al., 2012). They can defend homoeothermy through physiological mechanisms, such as evaporative cooling and controlled hyperthermia (Tieleman and Williams, 1999), as well as behavioural avoidance of heat gain, such as reducing activity and shade seeking (Cunningham et al., 2015). The warming trend observed as a result of climate change, however, will cause desert species to experience extreme high T_as more frequently and for longer periods at a time (Butt et al., 2016). This will result in some species living closer to the limits of their thermal tolerances (Parmesan and Yohe, 2003; Simmons et al., 2004). Desert-dwelling species are therefore expected to be among the first to reach the limit of their thermoregulatory capacities (Williams and Tieleman, 2005), making them suitable objects for studies on the impacts of climate change (McKechnie et al., 2012).

In order to predict the responses of desert birds to climate change, many researchers focus on the current trade-offs experienced by desert birds on hot days (Tieleman et al., 2008; Dean et al., 2009; Cunningham et al., 2013b). For example, if birds spend more time performing heat dissipation behaviours (e.g., panting and wing-drooping), then this may have repercussions for the time they can spend on other activities, such as foraging (Weathers et al., 1984; Wong and Candolin, 2015). A study on desert-living Southern Pied Babblers (*Turdoides bicolor*) showed panting behaviour performed while foraging led to a decrease in the ability to catch prey items. As a result, on hot days (T_a > 36.5 °C) these babblers were unable to maintain body mass (M_b) (du Plessis et al., 2012). In another study on Common Fiscals (*Lanius collaris*), birds were observed to continue foraging on hot days (T_a > 35 °C), but changed from their favoured high and exposed perches to more shaded locations: this change in behaviour resulted in lower prey capture rates (Cunningham et al., 2015). These impacts of high T_as were observed in mature birds, however during the breeding season these adults have to provision dependent offspring. Regulation of body water content by birds residing in arid environments requires a continuous balance of water intake (via food) and water loss (via evaporation) to cool down (Webster, 1991). This tight balance comes under even more pressure during periods of high energy demand, such as during the breeding season (Wolf, 2000). Low foraging efficiency will lead to lower chick provisioning rates and this may in turn affect chick growth rates and reproductive success (Tremblay et al., 2005; Cunningham et al., 2013c; Morrison et al., 2016).

1.4 Reproduction in desert birds

Reproductive costs are exacerbated by the influence of extreme arid conditions, causing reproductive rates generally to be low in desert-dwelling birds when compared to birds residing in mesic habitats (Williams and Tieleman, 2002). The current study will focus on the impacts of high T_a on reproductive success during both the incubation and chick rearing phases. Birds' eggs need to be protected from high T_as during incubation, as a reduction of the water content of the eggs could affect their viability (Ar and Rahn, 1980). Kentish plovers (*Charadrius alexandrines*) in the Arabian Desert were observed to increase cooperative incubation on hot days to lower the thermoregulatory cost per individual (Alrashidi et al., 2010). A similar pattern was observed in pairs of Hoopoe Larks (*Alaemon alaudipes*) who shared incubation duties equally during hot desert days to reduce their evaporative water requirements while protecting the eggs (Tieleman et al., 2008). Without this level of incubation effort, short interruptions of nest attendance by incubating adults could harm the developing chick inside the egg during hot weather events (Grant, 1982). Long periods with high T_as can also negatively affect chick growth and fledging success as observed in Common Fiscals (Cunningham et al., 2013c),

Southern Pied Babblers (Wiley and Ridley, 2016) and Sage Sparrows (*Amphispiza belli*) (Rotenberry and Wiens, 1991). On hot days, breeding birds make behavioural adjustments to minimise evaporative water losses of the eggs and chicks, but they also need to maintain their own water balance. An increase in the number of hot days during the breeding season is likely to increase energy expenses and water losses, lowering the reproductive rates of desert birds.

1.5 The Southern Yellow-billed Hornbill as the model species

This study explores the vulnerability of a desert-dwelling population of Southern Yellow-billed Hornbills, *Tockus leucomelas* (Lichtenstein, 1842). This species, although currently listed with a conservation status of "Least Concern" (Birdlife International., 2012), has been flagged as potentially vulnerable to a changing climate (Klaassen et al., 2003). The species, whose range extends into some of the hottest parts of southern Africa, is potentially sensitive to climate change because of its unusual breeding strategy (Hockey et al., 2005). With the exception of the two species in the genus *Bucorvus*, all hornbills in the Bucerotidae family, including the Southern Yellow-billed Hornbill, employ a similar breeding strategy, whereby the female seals herself in the nest cavity as a protective mechanism against predators (Moreau and Moreau, 1941; Witmer, 1993; Kemp, 1995). During incubation and part of the nestling period the females are confined to the nest and, as a consequence, the male hornbills are solely responsible for the provision of food to the females and chicks (Klaassen et al., 2003). The increase in the number of hot days observed in the Kalahari is expected to have implications for the reproductive success of the hornbills due to increases in heat load on the male hornbill and on the confined females and brood inside the nest.

I hypothesise that the increased heat load on male hornbills could affect their need for heat dissipation behaviour, with the potential to negatively impact their foraging effort and / or efficiency, as has been shown in other species (Fuller et al., 2014; Moyer-Horner et al., 2015). A potential decrease in foraging performance, whether mediated through changes in foraging effort or efficiency, could result in a decrease in male body condition (if males prioritise maintaining provisioning rates) or a decrease in provisioning rate (if males prioritise their own body condition maintenance) or both. Like the males, the females' maternal investments may be compromised during hot weather if they prioritise their own body condition by sacrificing the brood to ensure their own survival. So far, the linkages between those variables are unknown and it is of interest to conservation-management decisions to understand the impacts of climate change on the species. The outcomes of this study will also expand our understanding of the impacts of thermoregulatory trade-offs experienced by animals breeding under extreme hot conditions. Although other species might have the advantage of the biparental care system,

and the lack of protection against predators in open-cup nests, I expect similar reproductive constraints caused by thermoregulatory trade-offs made by the parents (Cunningham et al., 2013c).

Aspects of Southern Yellow-billed Hornbill ecology pertinent to this study are as follows. The species' preferred habitat is open woodland and well-vegetated patches of semi-arid savanna (Kemp, 1995), meaning that the study population inhabits the extreme arid part of their distribution. It is abundant and widespread, with the population size in southern Mozambique alone estimated to be over one million (Parker, 1999). The range of the species extends from southern Angola, southern Zambia and southern Malawi, south to central Namibia and northern and eastern South Africa (Hockey et al., 2005) (Figure 2). The longevity of the species in the wild is unknown, but is expected to be long-lived, as one male in captivity was recorded to be 23 years of age (Strehlow, 2001). The social system of the species is non-cooperative and pairs are territorial while breeding (Gonzalez et al., 2013). They are known to form flocks during the non-breeding period (Kemp, 1995). Common predators of adult hornbills in the southern Kalahari region are Bateleur (*Terathopius ecaudatus*) and Verreaux's Eagle-owl (*Bubo lacteus*) (Kemp, 1976). In Daan Viljoen GP, Namibia, chicks were observed to fall prey to Chacma Baboon (*Papio ursinus*) and Rock Monitor (*Varanus exanthematicus*) (Hockey et al., 2005). At the study site, I observed chicks being predated by Slender Mongoose (*Galerella sanguinea*) and Cape Cobra (*Naja nivea*) when they were incapable of re-sealing the entrance after female departure from the nest.

Southern Yellow-billed Hornbills are socially monogamous and at the beginning of the breeding season the hornbills spend most of their time pair-bonding through interaction and courtship displays (Kemp, 1995). Behaviours that are most often seen are allopreening and allo-feeding, leading to ritualised courtship feeding by the males to the females (Kemp, 1995). Once bonds are reinforced, the pairs prospect for suitable nesting trees with cavities. The females inspect the inside of the cavity and are responsible for the application of the nest seal (Myers, 2000). The males provide material for this seal which includes soil, bark and faeces. The females, once sealed in the nest, receive food from the males and provision this to the chicks (Mills et al., 2005). During the time the females are sealed inside the nest, they undergo a complete moult of the flight feathers and are thus totally dependent on the males, because even if they could break free of the nest, they would be unlikely to survive in a flightless state (Kemp, 1969). This scenario requires a significantly elevated work rate by the males above that which would be needed in a system of biparental care.

Egg laying commences 4 - 6 days after the female Southern Yellow-billed Hornbills enter the nest and eggs are laid at an interval of ~ 2 days (Hockey et al., 2005). Incubation starts with the first-laid egg and therefore the eggs hatch asynchronously after an incubation period of approximately 24 days (Kemp, 1995). Clutch size ranges between 2 to 6 eggs (Hockey et al., 2005). Among hornbills, infanticide and cannibalism of eggs and / or the youngest chick(s) are reported as common phenomena (Chan et al., 2007; Ng et al., 2011). The females consume eggs and chicks or feed the younger chick to the older chicks, potentially in response to low provisioning rates by the males. This behaviour is thought to be an adaptive strategy which increases the female's own body condition or the fledging success of the surviving offspring (Finnie, 2012).

At the study site in the Kalahari Desert, the Southern Yellow-billed Hornbills attempt a single brood annually during the breeding season. A prior study of the birds in this population suggests that the females are confined to the nest for an average period of 53.3 days (41 – 61) and leave the nest only when the chicks are large enough to reach for food at the nest opening (Finnie, 2012). After the females leave, the chicks re-seal the opening and the females help the males with chick provisioning (Kemp, 1976). In the Kalahari, Southern Yellow-billed Hornbills breed at the onset of summer, presumably linked to the rainy season and the increase in food availability (Finnie, 2012).

1.6 Introduction to the study site and population

The study population is situated on a 3500 ha private reserve (Kuruman River Reserve; 26°58′ S, 21°49′ E) in the Northern Cape of South Africa, in the southern Kalahari Desert (Figure 2). The vegetation comprises arid grassland with scattered shrubs on red sand dunes, with tall trees like *Vachellia erioloba* (~ 15 m), *Vachellia haematoxylon* (~ 10 m), *Boscia albitrunca* (~ 10 m), and *Ziziphus mucronata* (~ 8 m) along the dry bed of the Kuruman River. The hornbills mostly occur along the dry riverbed, where breeding takes place in natural tree cavities and in artificial nest boxes (Figure 2). The region experiences summer rainfall from December to March with a mean annual rainfall of 186.2 ± SD 87.5 mm and mean daily summer maximum air temperatures (T_{max}) of 34.2 ± SD 9.7 °C (1995 – 2015, Van Zylsrus weather station, SAWS). During the course of my study, a weather station (Vantage Pro2, Davis Instruments, Hayward, U.S.A.) was placed on the reserve, and set to record T_a (°C), wind speed ($m.s^{-1}$) and solar radiation ($W.m^{-2}$) at 5-min intervals.

This population of Southern Yellow-billed Hornbills had already been studied from 2008 – 2011 (Finnie, 2012) and most birds were tolerant of being followed by observers within 5 – 20 m,

facilitating the collection of observational data. Hornbills at the study site form pairs and breed between October and March (Finnie, 2012). Most of the hornbill pairs at the Kuruman River Reserve make use of artificial nest boxes and birds are fitted with colour rings for individual identification. One male was observed to breed during seven consecutive seasons (2009 – 2016) and one female that hatched in 2012 was first observed to breed in 2016: both records provide support that the species is relatively long-lived in the wild (as well as in captivity, Strehlow, 2001). The use of nest boxes by the birds allowed me access to the nest for collection of morphometric data of females and chicks, and placement of cameras, climate-recording devices and perch scales (further information on these methods is given in the following chapters).

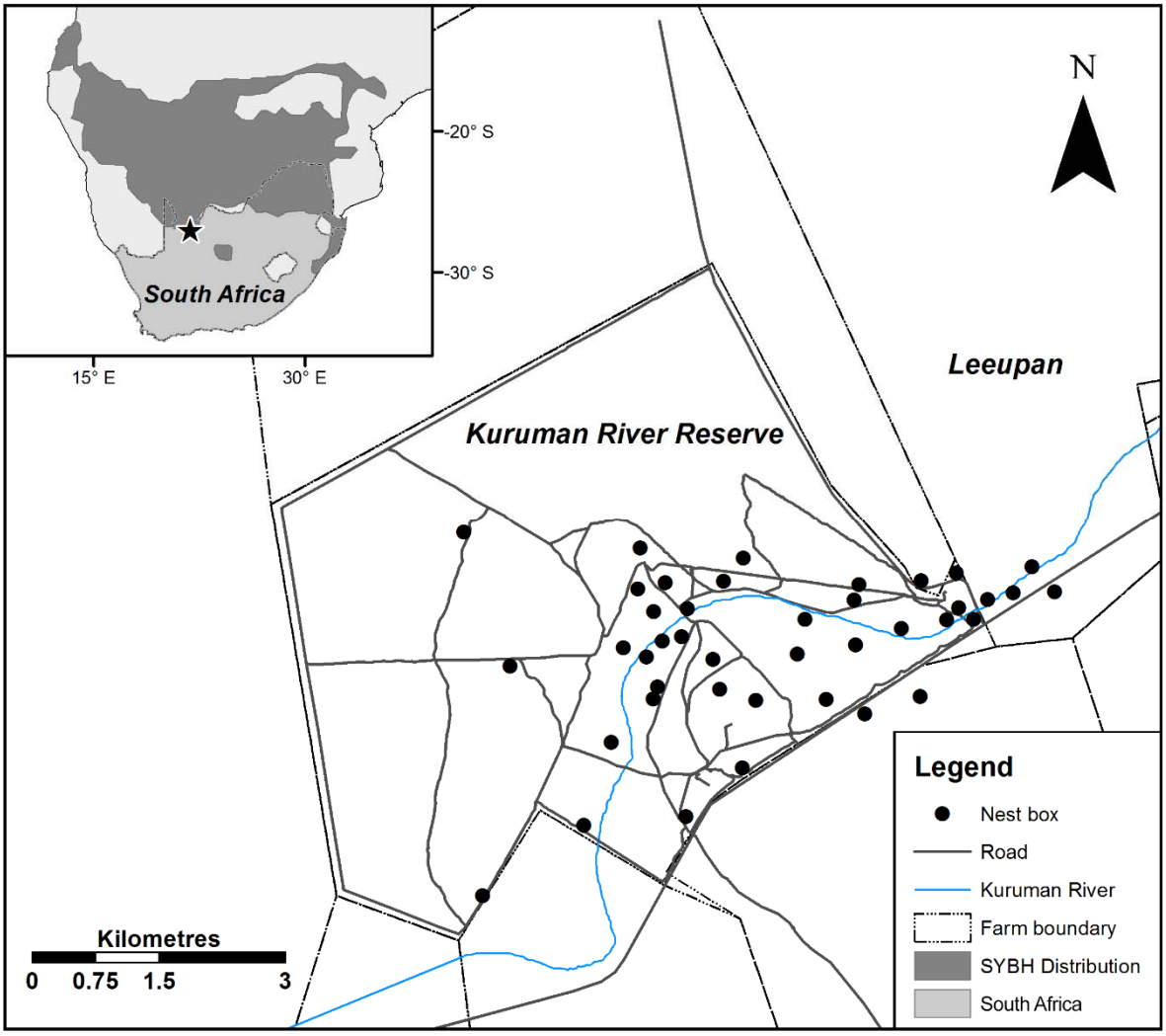

Figure 2 Map of the Kuruman River Reserve and the distribution of nest boxes (black dots) along the dry riverbed of the Kuruman River. Data collection for Chapters 2 – 4 and 6 took place on Kuruman River Reserve, whereas data collection for Chapter 5 took place at the neighbouring property 'Leeupan' – marked on the map. Inset: Southern Yellow-billed Hornbill distribution within southern Africa (dark grey shading) and location of the study site (marked with a star) within South Africa (light grey shading).

1.7 Objective

The objective of this research is to understand how thermoregulatory trade-offs mediate the response of desert organisms to hot temperatures and how this might affect their fitness under climate change, using a species with highly asymmetrical parental investment as a model. High T_as have been shown to affect reproductive performance of desert-living birds due to the trade-offs made between brood investment and thermoregulatory behaviour (Cunningham et al., 2013c). Among desert-living birds, hornbills are thought to be particularly vulnerable to high T_as due to their unusual breeding system which places high energy demands on the provisioning males and the confined females. The impact of high T_a on the reproductive performance is expected to be pronounced in the Southern Yellow-billed Hornbill which makes them a suitable study species. Therefore, I studied the relationship between the thermal environment and the reproductive performance of Southern Yellow-billed Hornbills in the southern Kalahari across three breeding seasons. This study addresses the direct and indirect effects of T_a on the fitness of both male and female adult hornbills and their offspring, through multiple observational and experimental techniques. The results of this study will provide insight into the behavioural and physiological capacity of this species to persist in the Kalahari with future increases in the frequency, duration and intensity of hot weather events.

1.8 Aims

I address the objective above in five data chapters with the following aims and research questions:

CHAPTER 2:

- AIM: To assess whether high T_as drive changes in behavioural patterns and landscape use in breeding male Southern Yellow-billed Hornbills, and how these processes affect foraging success.

- Do male hornbills use thermoregulatory behaviours in response to high T_as?
- Do high T_as impact the foraging effort and efficiency of male hornbills?

CHAPTER 3:

- AIM: To investigate the provisioning rate and allocation of dietary items to self *versus* nest by breeding male hornbills and the influence of T_a, M_b and diurnal M_b changes on their allocation decisions.

- Do high T_as influence male decisions regarding food allocation?
- Does male provisioning effort decline with increasing T_a?

- Do high T_as affect the M_b of breeding males?

CHAPTER 4:

- AIM: To establish if T_a influences female M_b and chick growth during the nesting period and ultimately the successful fledging of chicks.

- Do high T_as affect the M_b of breeding females?
- Do high T_as affect diurnal mass changes of females and nestlings?
- Does chick growth rate affect fledging success?
- Does T_{max} during the nesting period have repercussions for chick mass and tarsus length at fledging?
- Is nesting success affected by female M_b at the start of the nesting period?
- Does mean T_{max} during the nesting period affect the probability of nesting success?

CHAPTER 5:

- AIM: To assess whether the beak of this Afrotropical hornbill is functionally similar in terms of heat flux capacities to that of the Neotropical Toco Toucan (*Ramphastos toco*).

- What is the proportion of non-evaporative heat loss via the beak to total body heat loss?

CHAPTER 6:

- AIM: To compare data collected during this study with data collected by Finnie (2012) between 2008 - 2011, in order to understand a) whether climatic impacts on breeding success are already visible over a short time scale (2008 – 2015) and b) how T_a and rainfall affect breeding success at annual and population scale.

- Is there evidence of a warming trend at the study site?
- Does rainfall influence the timing of breeding?
- Do rainfall and T_a affect the total number of breeding attempts per season?
- Do rainfall and T_a affect reproductive success?

1.9 Thesis structure

In this thesis, I investigate the impacts of high T_as and rainfall on the reproductive success of desert-dwelling Southern Yellow-billed Hornbills. I carry out behavioural observations on provisioning male hornbills, I collect morphological measurements of females and chicks in the nest, I experimentally assess the importance of the hornbill beak to total heat dissipation and

continuously record the weather variables at the study site. The chapters of this thesis are structured to provide a logical flow ('story') of the hornbill reproductive system and the specific variables concerned (Figure 3).

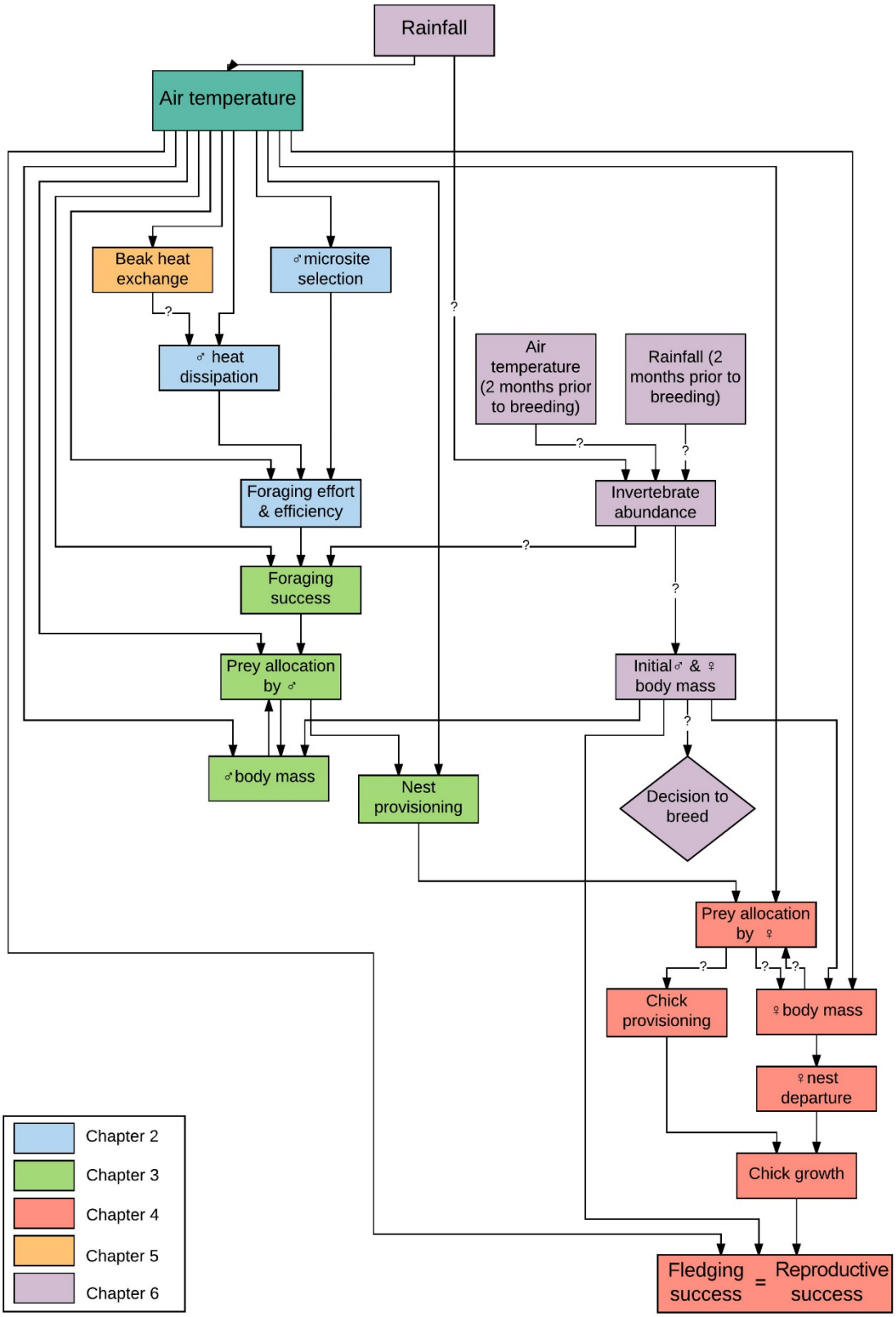

Figure 3 Flowchart indicating the relationships between the variables covered in this thesis. Solid lines indicate relationships explicitly tested in this study, lines with question marks indicate hypothesised relationships that were not assessed in this study. Colours highlight the chapter in which the particular variables were covered.

In Chapter 2, I assess how panting behaviour and microsite selection in male Southern Yellow-billed Hornbills affects their foraging efficiency, and how male M_b is affected by T_a. In Chapter 3, I examine how T_a influences male foraging efficiency, prey allocation decisions, provisioning effort and male M_b. In Chapter 4, I assess how the thermal environment affects female M_b and chick growth during the nesting period and I identify the variables that affect nesting success. In Chapter 5, I quantify the capacity for non-evaporative heat loss via the hornbill beak via thermal imaging by exposing hornbills to a gradient of T_as in a temperature cabinet. In Chapter 6, I investigate the impact of rainfall and high T_a on hornbill reproductive success by comparing the results of the current study with the findings of a previous study carried out on the same population of Southern Yellow-billed Hornbills. Lastly, in Chapter 7, I synthesise the findings of this thesis and discuss the implications of this study to our understanding of the vulnerability to climate change of Southern Yellow-billed Hornbills breeding in desert ecosystems.

List of symbols and abbreviations

T_a	air temperature
T_{min}	daily minimum air temperature
T_{max}	daily maximum air temperature
T_b	body temperature
T_e	operative temperature
T_{es}	standard operative temperature
T_s	surface temperature
T_{s_beak}	beak surface temperature
T_{s_skin}	skin surface temperature
T_{s_torso}	torso surface temperature
M_b	body mass
Ivlev *Ei*	Ivlev's electivity index

List of symbols and abbreviations used throughout this thesis.

CHAPTER 2 BEHAVIOURAL THERMOREGULATION CHANGES TIME-ACTIVITY BUDGETS AND LIMITS FORAGING EFFICIENCY IN MALE HORNBILLS

2.1 Abstract

A great thermal load is placed upon birds residing in hot environments, especially those breeding at the hottest time of year. Birds dissipate heat via panting and other avenues of evaporation when operative temperature (T_e; a measure of thermal load experienced by the bird as a result of all the combined heat sources and losses in its environment) approaches or exceeds body temperature (T_b). The high cost of evaporative water loss induces birds to perform other thermoregulatory behaviours, like shade-seeking and reducing activity. I compared microsite selection and time-activity budgets between 'cool' and 'hot days'. I assessed heat dissipation behaviour and its impact on foraging efficiency. Furthermore, I modelled foraging effort in relation to air temperature (T_a) and foraging efficiency in relation to the proportion of time spent panting and microsite use, and I assessed the impact of T_a on foraging success.

Heat dissipation behaviour was positively correlated with T_a and males spent more than half of their time panting when T_a > 34.5 °C. T_e decreased with increasing distance from the ground and was 6.4 – 12.8 °C higher in microsites exposed to the sun compared to shaded sites. Males avoided sunny microsites on the ground and preferred shaded and off-ground microsites especially on hot afternoons. Behavioural patterns changed between cool and hot days. On hot days the birds allocated 14.4 % more time to foraging in mornings and afternoons and were 14.5 % more inactive at midday of hot days as compared to cool days. While panting, birds caught 41.9 % less prey items per minute foraging than when not panting.

Male hornbills adjusted their behaviour during high T_as by becoming more inactive, thereby sacrificing territorial and comfort behaviour. Increased foraging effort was observed during the morning and afternoon on hot days. During midday foraging, that was reduced on hot days, most of the time was spent panting, and this reduced the overall daily foraging budget. This suggests that the total energy and water content of the prey caught might not have been sufficient to meet the thermoregulatory demands (increased need for water-rich prey items) of the males and the dependent females and brood inside the nest.

2.2 Introduction

Desert-dwelling birds make excellent models to test the impacts of high environmental temperatures on organismal performance, because these birds likely already live close to their upper thermal tolerances (McKechnie et al., 2012). The thermal tolerance to the environment by endotherms is limited by their capacity for thermoregulation (Schmidt-Nielsen, 1997). Controlled elevation of body temperature (T_b) (i.e., facultative hyperthermia) in endotherms is one thermoregulatory mechanism that allows animals to maintain a thermal gradient between T_b and T_a for passive heat dissipation during periods of high T_a (Tieleman and Williams, 1999). Extreme high T_b, however, can affect crucial physiological processes at cellular level with potentially lethal consequences (Schmidt-Nielsen, 1997; Portner, 2001). In birds, the necessity of maintaining T_b at sublethal levels is the basis for heat dissipation behaviours such as panting and wing drooping (West, 1965; Willmer et al., 2005). Panting promotes evaporative cooling and most non-passerines additionally lose heat via cutaneous evaporation or gular fluttering (Dawson, 1982). Heat loss via evaporation is an effective method of heat loss for those animals living in areas where water vapour densities are low (Gerson et al., 2014), but at the same time it is costly in desert habitats where surface water is scarce (Smit and McKechnie, 2015).

Behavioural changes, such as the use of thermally-buffered locations and reduced activity levels, can mitigate the physiological costs of keeping cool via reduction of evaporative water loss (Scheffers et al., 2014; Carroll et al., 2015; Martin et al., 2015). Microclimates vary on a small scale (Rosenberg et al., 1983), and are correlated with vegetation structure and topography (Suggitt et al., 2011). Locations within the landscape potentially being used by animals and characterised by certain climatic conditions are referred to as ‘microsites’ (Wooten et al., 1975). The limited vegetation in a desert landscape provides a range of potential thermal refugia that can be quantified according to exposure to the sun (influenced by vegetation cover) and height categories (Wolf et al., 1996; Seymour and Dean, 2010; Camacho et al., 2015). Differences in operative temperature (T_e; a measure of thermal load experienced by the bird (Bakken, 1992) between sunny and shaded sites can be as much as 12 °C, and are generally greater for smaller species (Wolf and Walsberg, 1996). Animals are likely to become more selective in the way they use the landscape as thermal conditions become more severe and the number of favourable microsites decreases (van Beest et al., 2012). For example, in the southwest USA two small desert bird species: the Verdin (*Auriparus flaviceps*) and the Blacktailed Gnatcatcher (*Polioptila melanura*) occupy tree crevices during the hottest times of day to reduce their total evaporative water loss (Wolf et al., 1996). Birds also limit their activity levels on hot days to reduce metabolic heat production (Goldstein, 1984; Speakman and Krol,

2010). Changes in behavioural patterns are therefore expected as a consequence of changing thermoregulatory demands (Martin et al., 2015).

Behavioural changes in response to high T_a include selection of thermal refugia which can have knock-on effects for other behaviours like foraging. Any behavioural responses to rising T_as may have important impacts on fitness, as even small changes to activity patterns can induce trade-offs that directly impact foraging, reproduction, territoriality, etc. (Wuethrich, 2000; Visser, 2008; Kearney et al., 2009). Du Plessis et al. (2012) found that heat dissipation behaviour in a population of desert-dwelling Southern Pied Babblers (*Turdoides bicolor*) significantly decreased foraging efficiency, despite unchanged foraging effort, and Cunningham et al. (2015) found that changes in microsite use halved prey capture rates in breeding Common Fiscals (*Lanius collaris*). In the context of reproduction, high air temperatures (T_as) can cause birds to make trade-offs between thermoregulation and incubation effort (Alrashidi et al., 2010), nest site location (Tieleman et al., 2008) and provisioning effort (Winkler et al., 2002; Cunningham et al., 2013c). Only few studies have focused on the association between heat dissipation behaviour, spatial use and foraging efficiency, and how the interplay between these factors is affected by T_a (Kearney and Porter, 2009; Cunningham et al., 2015). Linking spatial use, behaviour and time-activity budgets in response to the thermal landscape can reveal the costs and benefits of using thermal refugia in physiologically challenging environments (Bennett et al., 1984; Oswald and Arnold, 2012; van Beest et al., 2012). Therefore, understanding fine-scale landscape use by animals provides information on current microsite quality and can be used to predict sensitivity of species to future climate change scenarios (Suggitt et al., 2011; Hovick et al., 2014).

In this chapter I investigate whether high T_as drive changes in behavioural patterns and landscape use in breeding male Southern Yellow-billed Hornbills (*Tockus leucomelas*). In order to assess whether landscape use was associated with thermoregulatory requirements, I estimated heat loads (measured via T_e) experienced by hornbills in each microsite. I predicted that males would spend more time in shaded microsites during periods of high T_a and that this would limit their foraging opportunities. I quantified heat dissipation behaviours (panting, wing-drooping) and microsite selection in relation to T_a and time of day, and I assessed foraging effort, foraging efficiency and foraging success in relation to T_a, the age of the nestlings, microsite use and the proportion of time spent panting. I also predicted that during very hot weather, increases in time allocation to heat dissipation behaviours would result in reduced foraging efficiency, reflecting behavioural trade-offs and missed foraging opportunities.

2.3 Methods

2.3.1. Study site and population

I observed semi-habituated, male Southern Yellow-billed Hornbills at the Kuruman River Reserve (26°85' S, 21°49' E). Observations took place in the austral summers (October to March) of 2012 / 13, 2013 / 14 and 2014 / 15 during the hornbills' breeding season which coincides with the highest annual temperatures. During this period, male hornbills are central place foragers (in proximity to the location of the nest) and are thus easy to find for observation. All data were collected from breeding males whose female partners and / or chicks were sealed within the nests. A weather station at the site recorded T_a (°C), wind speed ($m.s^{-1}$) and solar radiation ($W.m^{-2}$) at 5-min intervals throughout the study (Vantage Pro2, Davis Instruments, Hayward, U.S.A.). For a full description of the study site and population see Chapter 1.

2.3.2. Behavioural observations

During the three breeding seasons, I conducted 204 behavioural observations on 12 breeding male hornbills across 17 breeding attempts. Behaviour data were collected during 30-min continuous focal observations (hereafter called 'focals'), conducted at a randomly selected time within each of three diurnal time periods: morning (sunrise – 10h59), midday (11h00 – 14h59) and afternoon (15h00 – sunset). If I lost sight of a bird for longer than 5 min during a focal, the focal was discarded and a new focal was started once the bird was relocated. The aim was to collect one focal per diurnal period per individual on four days with different T_{max}s: cool (< 30 °C), warm (30 - 35 °C), hot (35 - 40 °C) and extreme (> 40 °C) during each of five reproductive stage periods: female only in the nest (incubation), first hatched chick between 0 – 10 days of age, 11 – 20 days of age, 21 days of age until date of female departure from the nest and chicks only (post female departure) (Table 1). Females departed the nest when chicks were aged 21.6 ± SD 3.3 (15 – 26) days, therefore sample sizes of focal observations when chicks > 3 weeks old with females still present were small (Table 1).

Table 1 Sample sizes of focal observations on breeding male Southern Yellow-billed Hornbills categorised per diurnal period (morning, midday, afternoon) and per nest stage (female incubating, chicks 0 – 10 days old, 11 – 20 days old, 21 days old – female departure, female departure – chick fledge). Focal observations were undertaken on 12 semi-habituated males over 17 breeding attempts across 3 breeding seasons.

	♀ incubating	0 - 10 days old	11 - 20 days old	21 days old - ♀ departure	♀ departure - chick fledge	*Total*
T_a range (°C)	20.6 - 38.4	17.8 - 38.0	20.6 - 39.9	26.6 - 38.9	19.1 - 40.1	
1: Morning	15	23	21	6	17	82
2: Midday	8	19	19	2	16	64
3: Afternoon	7	14	18	3	16	58
Total	*30*	*56*	*58*	*11*	*49*	*204*

Focal data were recorded using a digital voice recorder (ICR-FP550, SANYO Electric Co., Osaka, Japan) and later transcribed with a PDA (Trimble Juno 3D, Trimble Navigation Limited, Westminster, U.S.A.) into a custom built database using Cybertracker software (CyberTracker 3.372).

Weather conditions were recorded at the start of each focal: wind speed (zero, low, medium and high) and cloud cover (clear, some clouds and overcast). During focal observations, the position of the hornbill within the landscape was recorded continuously, categorised by height of perch (ground, 0 - 0.5 m, 0.5 – 1 m, 1 – 3 m and > 3 m) and exposure to the sun (exposed, dappled and shaded). “Exposed” referred to full exposure of the bird to the sun, “shaded” is fully shaded by vegetation or artificial objects and “dappled” denotes the bird having patches of shade and sun on his body. In addition, I distinguished between the following categories of behaviours: foraging, provisioning, territorial, comfort, inactive, and moving. Foraging behaviour was identified by searching behaviour where the birds would hop around and characteristically move their head and eyes to look for potential food items. Foraging method (cracking, probing, hawking, gleaning, and digging with the beak) and result (successful or unsuccessful) was included in foraging behaviour. Provisioning behaviour included the flight to the nest and the provisioning a food item. Territorial behaviour involved territorial calling and interactions with other species and Southern Yellow-billed Hornbills other than their mate. Comfort behaviour involved preening, and inactive behaviour referred to the males observing (scanning) the environment, resting and being vigilant. The category “moving” referred to walking on the ground, hopping in trees or flying. Heat dissipation behaviour (none, panting, wing drooping, and panting & wing drooping) was recorded during the entire focal and could occur concurrently with any of the behaviours described above. Panting behaviour was identified by an open beak and wing drooping by low hanging wings held away from the body, allowing convection underneath the wing.

2.3.3. Heat load measurement

Operative temperature (T_e) and standard operative temperature (T_{es}) can be used to describe the environmental temperature experienced by an individual as a single number parameter, integrating the influence of solar radiation, convection and T_a (Bakken et al., 1985). The advantage of using T_e or T_{es} rather than T_a (derived from weather stations) as a measure of heat load is that these measures describe more accurately the heat load upon the animal, by including aspects of the thermal properties of the microsite in which the animal is present, as well as thermally relevant parameters of the animal itself (e.g. size, shape, integument), in addition to T_a alone (Camacho et al., 2015).

The difference between T_e and T_{es} is that T_{es} includes a measure of the net heat production of the individual, which is computed by metabolic heat production (M) minus evaporative heat loss (M - E), hence providing an index of the challenge faced by the animal in maintaining a stable T_b. T_e does not include net heat production and can only approximate the external "heat load" experienced by the animal. Estimates of T_e and T_{es} can be modelled numerically (Moyer-Horner et al., 2015) or measured with taxidermic models of the species of interest (Bakken, 1976, 1992). T_{es} is often measured with heated taxidermic models, with the heating rate ($W.m^{-2}$) mimicking the energy the animal uses to keep T_b constant (Bakken, 1992). This method is suitable as long as T_{es} remains below the animal's usual T_b, and the taxidermic model requires energy input to maintain stable "T_b". T_{es} becomes difficult to measure once it exceeds the normal T_b of the animal. Measuring T_e using unheated models, like black globe thermometers (hereafter called 'blackbulbs') and taxidermic models, is therefore more practical than measuring T_{es} in the field, especially in hot environments like the southern Kalahari in summer. For this reason, I used T_e as a measure of heat load. Neither blackbulb nor taxidermic model methods are perfect as they do not take into account humidity or evaporative heat loss; however, both methods provide a better estimate of heat load than T_a alone.

2.3.4. Blackbulb placement, construction and calibration

T_e is best measured with a taxidermic model covered by a skin and pelage of the species of interest, in order to mimic the thermal properties of the species (Bakken, 1992). However, because it was impractical to obtain a large number of hornbill skins, I mapped the hornbills' thermal environment using 36 blackbulbs, and calibrated these against two taxidermic models (details below) (Bakken, 1980). Blackbulbs were deployed at the start of the study and programmed to log temperature continuously at 5-min intervals during the three study seasons. Three blackbulb replicates were placed at each height (ground, 0 - 1 m, 1 - 3 m and > 3 m)

and exposure category (exposed, dappled and shaded), such that T_e data were collected in microsites representative of the locations used by birds during focal observations.

The blackbulbs were constructed according to Bakken's (1985) black globe thermometer, 'rugged model', consisting of a copper sphere (painted black) with internally mounted temperature loggers (Thermochron iButton, DS1923, Maxim, Sunnyvale, CA, USA, resolution = 0.0625 °C, hereafter "iButtons") (Figure 1A). The diameter of each blackbulb approximated mean thoracic depth of an adult male Southern Yellow-billed Hornbill (60 mm), which was estimated from museum specimen measurements (mean 60.1 ± SD 5.6 mm, n = 15). The two taxidermic models were each made of a hollow copper spheroid and copper sheeting shaped to resemble the hornbill body shape and covered with a hornbill skin (following Wathes and Clark, (1981), Figure 1B). An iButton was placed in each of the taxidermic models.

Figure 1 (A) A blackbulb and (B) a Southern Yellow-billed Hornbill taxidermic model placed in an 'exposed' microsite at a height between 0 and 1 m.

Calibration was achieved by positioning three blackbulb replicas together with the two taxidermic models at locations representative of each of the 12 microsite categories over a period of 2 - 3 days per microsite category. The blackbulbs and models were carefully placed within the same microsite at a sufficient distance from each other in order to avoid them shading each other. The taxidermic models were positioned facing north in all microsites. During calibration, the iButtons within the taxidermic models and the blackbulbs were programmed to log temperature at 1-min intervals to obtain fine-scale data. The weather station also was programmed to record data at 1-min intervals while blackbulb calibration took place. In order to standardise field conditions, calibration was done over a range of T_as

between 20 and 40 °C on clear days only (solar radiation > 600 $W.m^{-2}$, n = 27) and at a low wind speed (< 5 $m.s^{-1}$), since low solar radiation (< 600 $W.m^{-2}$) and high wind speed (> 5 $m.s^{-1}$) were rare during the study period (1.5 % and 4.7 % of days during the study period, respectively). Wind speed and solar radiation were therefore not included in statistical calibration models.

More than 95 % of the variation in taxidermic model T_e could be explained by the blackbulb T_e in all microsite categories, and the relationship between the taxidermic model temperature and the blackbulb temperature was linear in all 12 microsite categories (Figure 2). Hereafter, the T_e reported will be a corrected blackbulb temperature obtained by adding the intercept value of the regression of taxidermic model temperatures against blackbulb temperatures for each microsite to the blackbulb temperature value and multiplying it by the slope estimate (intercepts and slopes presented in Figure 2).

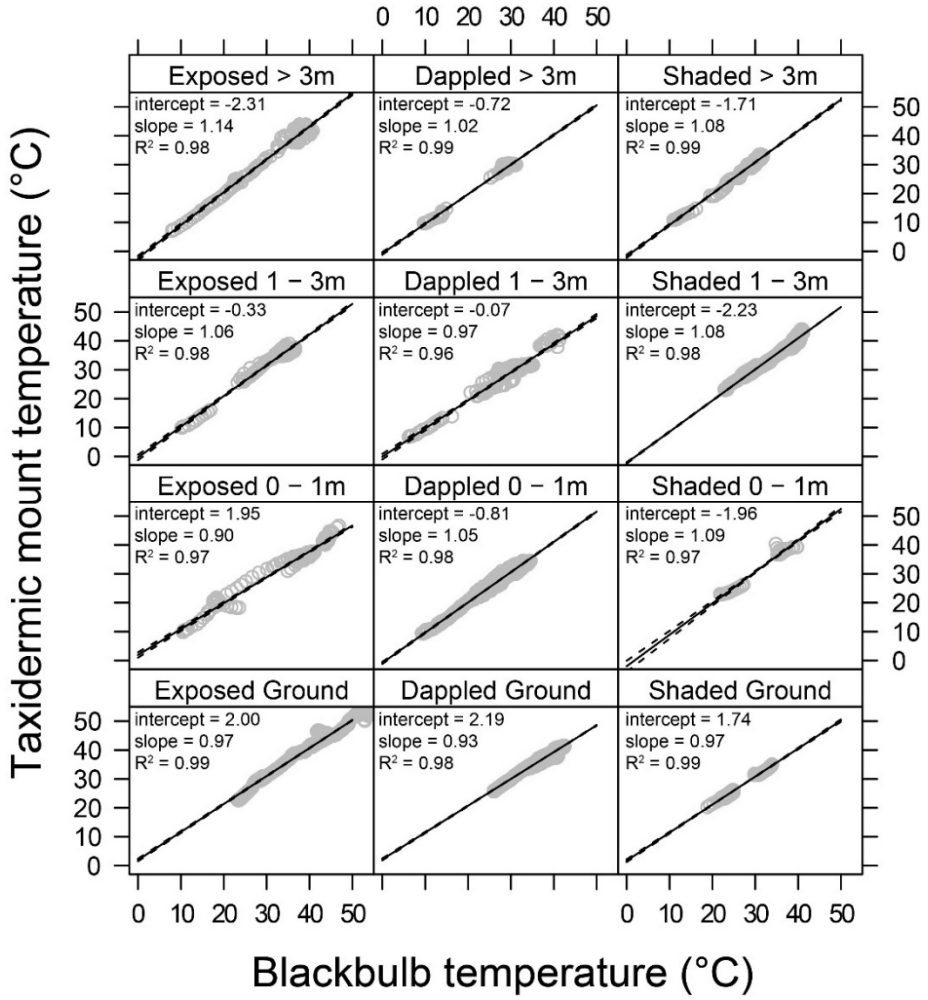

Figure 2 Calibration curves of taxidermic model temperature from blackbulb temperature in the 12 microsite categories. Data were obtained from the calibration of blackbulbs (n = 3) with taxidermic models (n = 2) over a total of 27 days. The data are represented as grey symbols, the black line represents the model fit and the dotted line represents the upper and lower 95 % CI.

Estimates of the intercept, the slope and the multiple r^2 value of the linear relationship are presented in each panel. The slope estimate refers to the change in taxidermic model temperature per 1 °C increase in blackbulb temperature.

2.3.5. Microsite availability

Microsite selection (preferred, avoided or used in keeping with availability) by each hornbill was assessed by comparing microsite use by each individual to the actual availability of these sites within their territory (Erickson et al., 2001; Thomas and Taylor, 2006; Seymour and Dean, 2010). During focal data collection, male hornbills foraged within a 1-km radius of the nest tree, therefore I estimated microsite availability by identifying potential perches (including on the ground) within a 1-km radius around the nest tree along a 10-m x 10-m grid overlaying the bird's territory. At every 10-m along each transect (i.e. grid intersection points), potential perches (bushes, trees, or fences) were identified within a 50-cm radius of the sampling point. A 4-m measuring pole was used to record the height of each potential perch and assign it to a height category. For each potential perch the level of exposure to the sun was estimated for each diurnal period; morning, midday and afternoon, taking into account changes in sun angle. Within each hornbill territory, I recorded at least 100 potential perch sites (range: 102 – 126 potential perch sites per territory, n = 12 territories). For each territory, I used these data to calculate the proportion of available microsites for each exposure, height and diurnal period. These were compared to the microsites actually used by the hornbills using Ivlev's Electivity Index (following Strauss (1979); described below under "Statistical analysis").

2.3.6. Statistical analysis

All statistical analyses were carried out in the R statistical environment using R Studio interface (R Development Core Team, 2016) with the core packages and packages lme4 (Bates et al., 2015) and MuMin (Bartoń, 2015). General linear mixed models (GLMM) and linear mixed models (LMM) were fitted by REML and normality of all model residuals was confirmed visually using a Normal Q-Q plot. Model selection was achieved using the Akaike Information Criterion corrected for small samples (AICc). I constructed a global model that consisted of all the variables I hypothesised to have an effect on the response variable. Best-fit models were chosen based on comparison of the corrected Akaike Information Criterion (AICc) between all possible nested models within the global models, using the "dredge" function in MuMin. All models with ΔAICc less than 2 were kept and I used model averaged estimation of effects, standard error and p-values when the set of best-fit models contained more than one model.

Random terms were included in each model to account for non-independence due to repeated measures of individuals and seasons. Prior to fitting global models, linear regression was used

to check for collinearity of the fixed variables and correlated variables were never included in the same model. Time of day (6h00 to 7h00) and diurnal period (morning, midday, afternoon) were both correlated with T_a and could therefore not be included within the same models as each other. I therefore compared AICc values of linear models for each response variable as a function of T_a, time of day and diurnal period, and included in subsequent global models the factor which best explained variation in the response variable according to AICc (i.e. had the lowest AICc). P-values < 0.05 were taken as statistically significant and data are presented as mean estimates ± 1 standard error (SE) unless otherwise stated.

Proportion of time spent panting

Time spent panting included panting behaviour with and without concurrent wing drooping and was calculated as a proportion of the focal time in minutes when the bird was in sight. A combined vector of 'proportion of panting behaviour' versus 'proportion of non-panting behaviour' was analysed using a GLMM with a binomial error distribution as a function of the predictor variable T_a (obtained from the onsite weather station) and 'individual' nested within 'season' was included as a random factor. From this model a threshold temperature was established at which the individuals spent 50 % of their time performing heat dissipation behaviour (referred to as the panting threshold temperature) by dividing the absolute value of the intercept by the absolute value of the predictor (beta) estimate (i.e., HD_{50}; Smit et al. (2016). The panting threshold temperature was chosen as an indicator above which thermoregulatory costs were high (as indicated by the fact that the birds were spending more than 50 % of their time performing heat dissipation behaviour) and was used to separate data into 'cool days' (days on which T_a did not exceed the panting threshold temperature) and 'hot days' (days on which T_a exceeded the panting threshold temperature) for further analyses of behavioural patterns and microsite use by hornbills. Sample size for this analysis was 204 focal observations collected from 12 male hornbills.

Correlation between operative and air temperature

The relationship between T_e and T_a was assessed per each of the 12 microsite categories per time of day (6h00 to 19h00). Based on the results of these correlations, the microsite categories were then simplified from 12 down to four categories as follows. The data from 'dappled' categories were added to the 'shaded' category for each height, and the height data were then combined into two categories: on ground and off-ground (a combination of all categories > 0 m). Mean T_e and T_a were then calculated per diurnal period (morning, midday, afternoon) for each of the four simplified microsite categories (exposed on ground, exposed

off-ground, shaded on ground and shaded off-ground). Sample size for this analysis was 441 days of T_e data collection.

Microsite preference using Ivlev's electivity index

Microsite selectivity was assessed using Ivlev's electivity index (*Ei*, (Strauss, 1979; Cunningham et al., 2015), which estimates whether a particular microsite is preferred or avoided in relation to its availability in the environment. I calculated an *Ei* value for each hornbill (n = 12) for each microsite category during each diurnal period and on cool and hot days. The index of selectivity *Ei* is calculated as:

$$Ei = (ri – Pi) / (ri + Pi)$$

where *ri* is the proportion of time a bird spent in a certain microsite and *Pi* is the proportion of available microsites of the same category in the bird's territory. The formula returns a value between -1 and 1, whereby negative values indicate avoidance of the microsite by the bird, zero indicates neither preferred nor avoided and positive values indicate preference / positive selection of a certain microsite type (i.e. used more than expected based on availability). Repeated measures on the same individual were dealt with by taking the average proportion of time spent in a certain microsite on cool or hot days per diurnal period per individual. A t-test was used to assess whether the mean Ivlev index across all the birds in the sample was significantly different from zero. A Wilcoxon rank sum test was used to assess whether there was a difference in preference for different microsites on cool versus hot days. The sample size for this analysis was 12 individual male hornbills in 12 different territories.

Behavioural patterns

The diversity of hornbills' behavioural repertoires were compared between cool and hot days using Shannon–Wiener diversity indices followed by a post hoc Hutcheson's t-test (Heip and Engels, 1974). Behavioural repertoires were compared across diurnal periods (morning, midday and afternoon) on cool and hot days to assess during which period differences in behaviour occurred. In order to account for repeated measures, I first averaged the time spent performing each of the behaviours per diurnal period on cool and hot days for each of the individual males. Sample size for this analysis was 204 focal observations collected from 12 male hornbills.

Foraging effort

The time spent foraging was drawn from the focal observations and calculated as a proportion of the total focal time when the bird was in sight. Comparison of the AICc values confirmed that the global model including the variable 'T_a' (AICc = 541.3) predicted the response variable 'foraging effort' better than the global model that included the variable 'time of day' (AICc = 546.5). A combined vector of 'proportion of time foraging' versus 'proportion of time not foraging' was analysed using a GLMM with a binomial error distribution as a function of the predictor variables T_a (obtained from the onsite weather station), nest stage ("chick age") and microsite. The age of the chicks was taken as the day of hatch of the first chick being 0. 'Individual ID', 'focal ID' and 'season' were included as random factors. Sample size for this analysis was 204 focal observations collected from 12 male hornbills.

Foraging efficiency

The number of prey captures per minute foraging was calculated as a function of time spent foraging to assess reliability of the collected data. Foraging attempts with a duration < 2.5 min had a high variation in the number of prey captures per minute, but stabilised once observations exceeded ~2.5 minutes in length (Figure 3). Foraging attempts shorter than 2.5-min were therefore excluded from subsequent analyses of foraging efficiency.

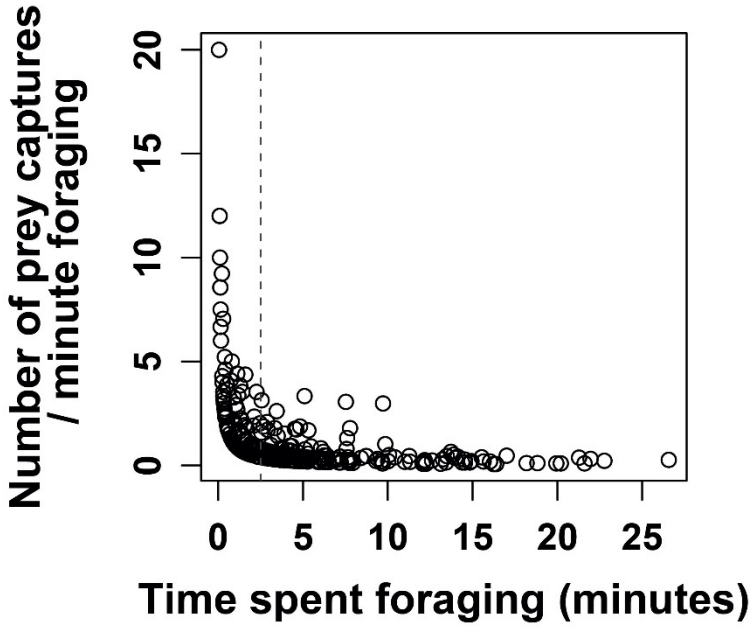

Figure 3 The number of prey captures per minute spent foraging of Southern Yellow-billed Hornbills. The vertical dashed line indicates 2.5-min.

Foraging efficiency (the number of prey captured per minute foraging) was analysed using a GLMM with a Poisson error distribution that included the fixed factors 'microsite' and a

combined vector of ‘proportion of time spent panting’ and ‘proportion of time spent not panting’. T_a was correlated with the proportion of time spent panting and could therefore not be included in this analysis. ‘Individual ID’, ‘focal ID’ and ‘season’ were included as random factors. Sample size for these analyses was 35 focal observations collected from 7 male hornbills.

The effect of heat dissipation behaviour on foraging efficiency was further assessed with a paired t-test by comparing the number of prey items captured by hornbills per minute foraging within the same diurnal period, while birds were panting versus while not panting. This analysis was carried out to assess the impact of panting behaviour itself on foraging efficiency, while excluding the potential effect of T_a, as T_a remained relatively constant within focals. Sample size for these analyses was 35 focal observations collected from 7 male hornbills.

Foraging success

Overall foraging success (prey captures per 30-min focal) as a function of T_a was modelled as a zero-inflated poisson regression using the statistical package pscl (Zeileis et al., 2008). A Vuong non-nested hypothesis test confirmed that the zero-inflated poisson model was superior to the standard Poisson model. The model type did not support inclusion of random factors. Therefore, the model is pseudoreplicated and caution was required when interpreting the results as p-values would be artificially small because of the pseudoreplication. Sample size for this analysis was 204 focal observations collected from 12 male hornbills.

2.4 Results

2.4.1. Proportion of time spent panting

The proportion of time a bird spent engaged in heat dissipation behaviour was positively correlated with T_a (GLMM estimate = 0.44 ± 0.14, z = 30.62, p <0.001). Birds began panting at T_as as low as 23.5 °C and the T_a at which individuals spent half of their time panting was 34.5 °C (Figure 4).

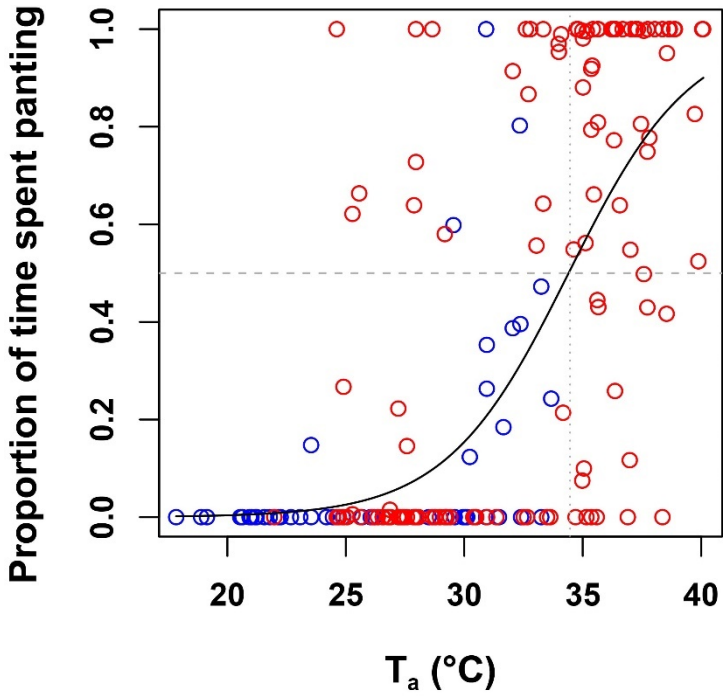

Figure 4 The proportion of time spent panting (heat dissipation via respiratory evaporative heat loss) as a function of T_a in male Southern Yellow-billed Hornbills on 'cool' days (blue symbols) and on 'hot' days (red symbols). The black line represents a logistic regression with a binomial error distribution that includes the variable T_a. Individual ID nested in season was included as a random factor. At T_a = 34.5 °C, individuals spent on average 50 % of their time panting as indicated by the grey dashed lines. Data were derived from 204 focal observations collected from 12 male hornbills.

The threshold temperature 34.5 °C was used as a representative temperature above which birds spent more than half their time engaged in respiratory evaporative water loss. Focal observations were collected on 69 cool days (T_{max} < 34.5 °C; range 17.8 – 34.4 °C) and on 135 hot days (T_{max} > 34.5 °C; range 34.5 - 40.1 °C).

2.4.2. Correlation between operative and air temperature

T_e consistently exceeded T_a at all microsites throughout the day, but this difference was greatest at midday (11h00 to 14h59; Figure 5). Hottest microsites were those close to the ground and / or exposed to the sun. T_e in exposed microsites exceeded the panting threshold temperature after 8h00 (approximately 2 hours after sunrise), whereas in shaded microsites this was only after 11h00.

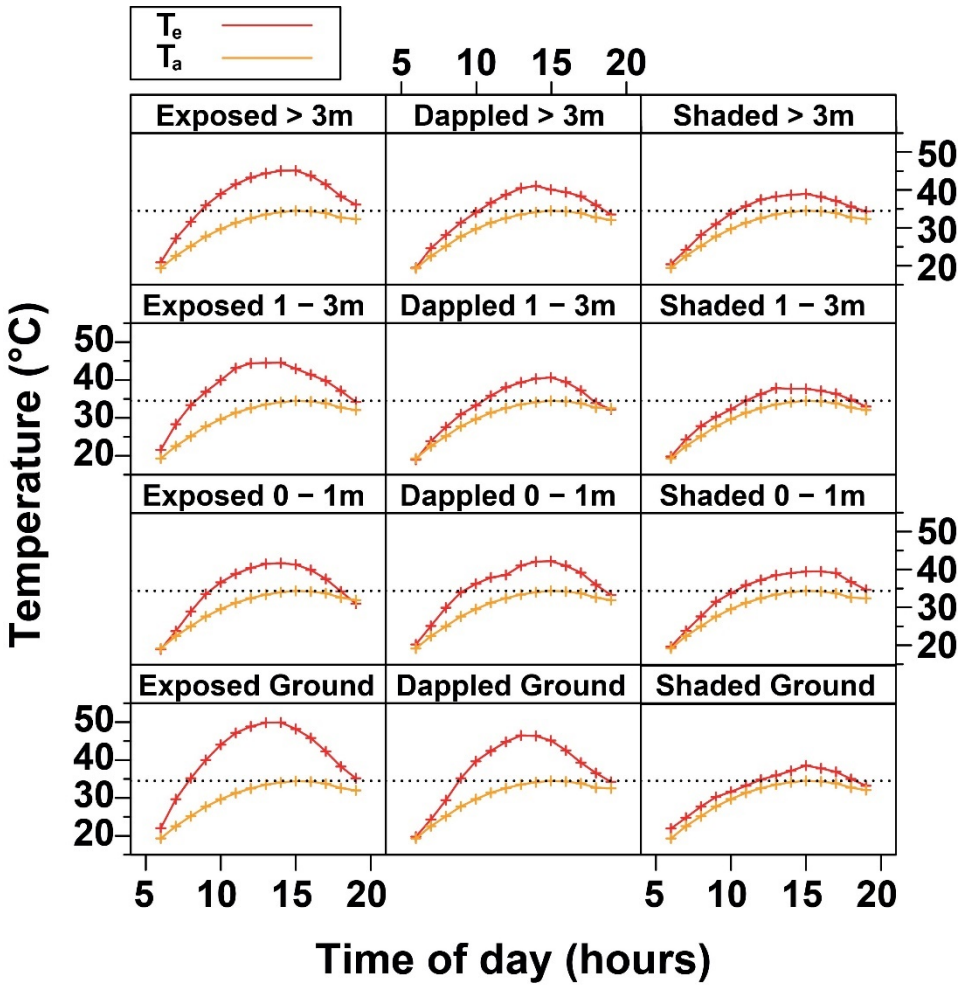

Figure 5 Mean T_e (°C) and mean T_a (°C) as a function of time of day (hours) expressed for each of the microsite categories used by Southern Yellow-billed Hornbills. Grey dashed line represents the 50 % panting threshold temperature at 34.5 °C. Data were derived from 441 days of T_e records from three calibrated blackbulb thermometers per microsite category. T_a data were derived from the onsite weather station over the same period.

The difference per microsite between T_a measured by the weather station and T_e measured by the calibrated blackbulbs, shows how the temperature experienced by the birds (T_e) at different T_a can vary according to the microsite they occupy. T_e was hottest in exposed microsites on the ground where temperatures reached up to 61.9 °C (mean 49.6 ± SD 6.3 °C) at 14h00, whereas T_e in shaded microsites on the ground at the same time were 39.3 ± SD 4.7 °C. T_e in the morning and afternoon differed less from T_a than during the middle of the day, likely due to the impact of solar radiation (Figure 6).

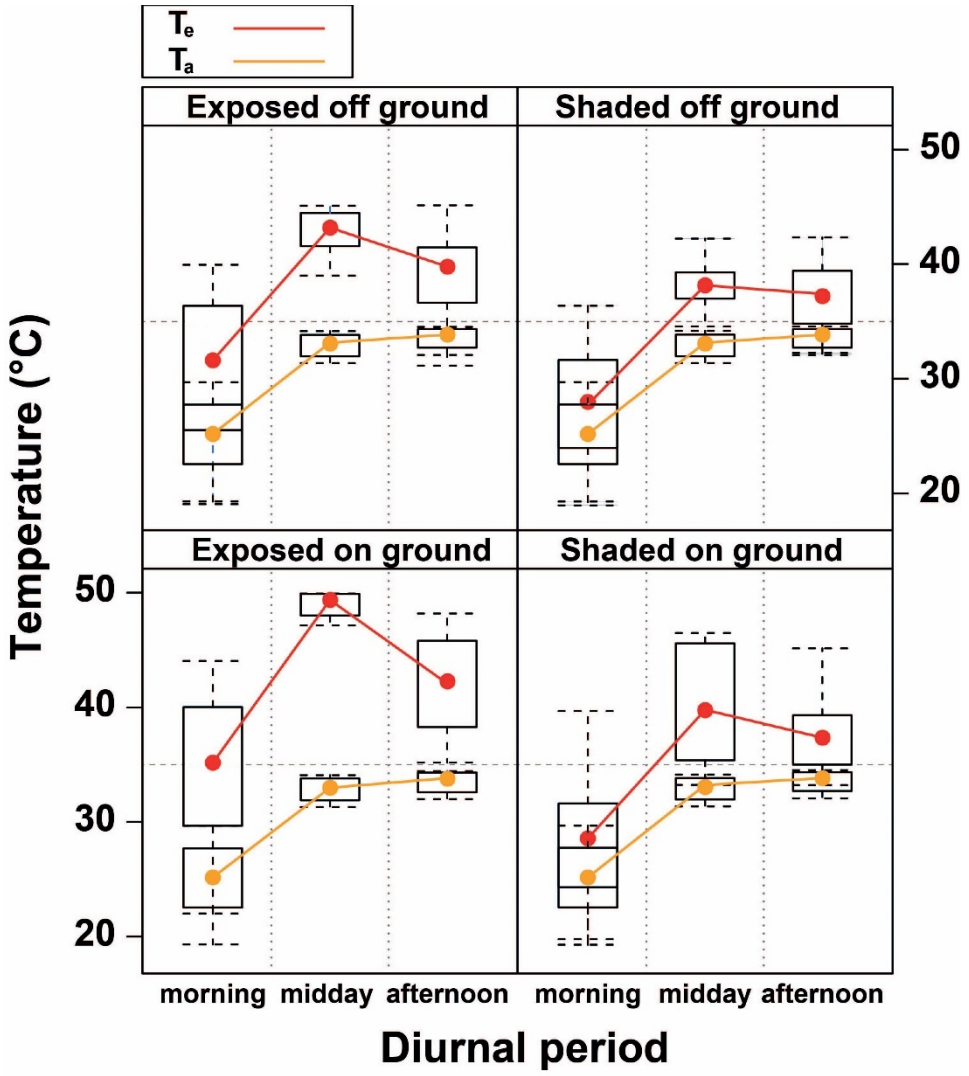

Figure 6 The interquartile range and median of T_e (°C) and T_a (°C) per diurnal period given for each of the four microsite categories. The greatest difference between T_e and T_a occurred in the category 'exposed, on ground' and the least difference in the 'shaded, off ground' microsite. T_e and T_a also deviated from one another in accordance to diurnal period, with the greatest difference during the midday diurnal period, and the least difference during the morning and afternoon diurnal periods. Grey horizontal dashed line represents the 50 % panting threshold temperature at 34.5 °C. T_e data were derived from 441 days of T_e records from 36 blackbulbs, and T_a data were derived from the onsite weather station over the same period.

2.4.3. Microsite preference

Shaded microsites off the ground were significantly preferred at midday on cool days and at midday and all afternoon on hot days (Figure 7; Table 2). Exposed microsites on the ground were significantly avoided during all diurnal periods on both cool and hot days (Figure 7; Table 2).

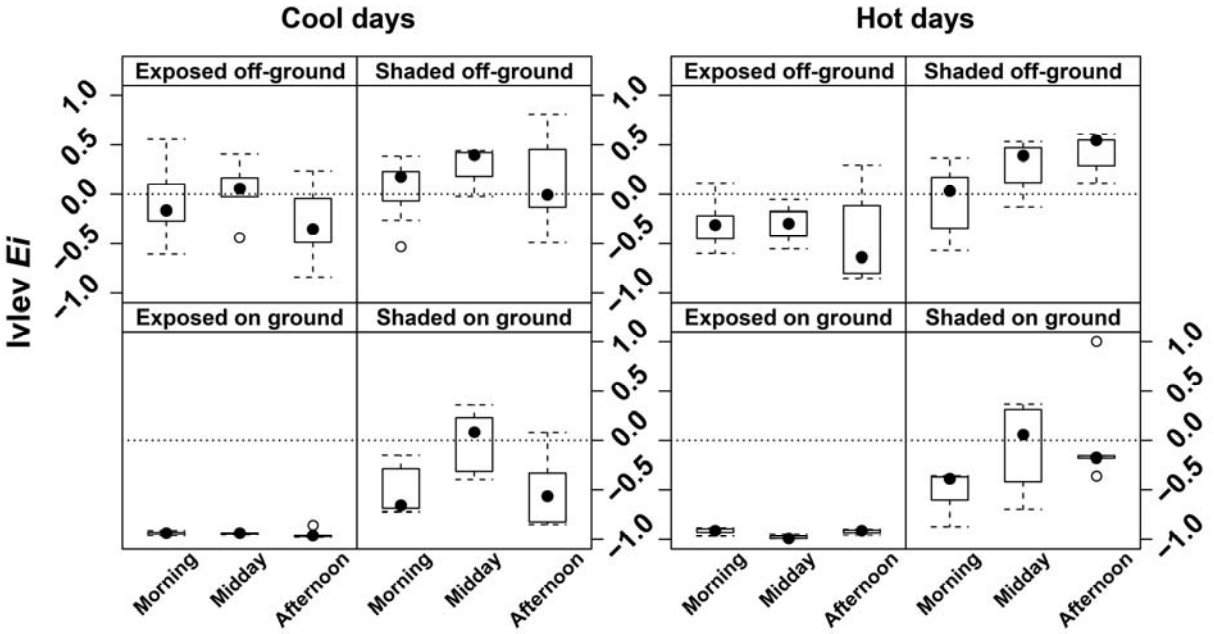

Figure 7 Ivlev's electivity index (*Ei*) given for 'cool days' (T_{max} < 34.5 °C) and 'hot days' (T_{max} > 34.5 °C) for each diurnal period and microsite type. Values < 0 indicate avoidance of the microsite, values > 0 indicate preference of the microsite. On cool days exposed microsites off ground are marginally preferred during the midday diurnal period, on hot days these are avoided. Shaded microsites off ground are neither preferred nor avoided during the morning and afternoon on cool days, but are marginally preferred at midday. On hot days, shaded microsites off the ground are marginally preferred at midday and preferred during the afternoon period. Ivlev *Ei* was calculated from 12 individuals in 12 different territories.

Shaded, on ground microsites were avoided during the morning on both hot and cool days, although to a significantly lesser extent in the morning on hot days in comparison with cool days. Exposed and shaded microsites on the ground were avoided to a significantly lesser extent on hot afternoons in comparison with cool afternoons. Shaded sites off ground were significantly more preferred on hot days in comparison with the afternoon on cool days (Table 2 and Table 3).

Table 2 Selected microsites in proportion of total used by the birds and the available microsites in proportion to total available in territory, preference (+) or avoidance (-) of each microsite, Pearson's chi-squared value of goodness-of-fit, *Ei* value and *Ei* significance given per diurnal period (morning, midday and afternoon), exposure (exposed, shaded) and height category (on ground, off-ground) of each microsite on cool days (T_{max} < 34.5 °C) and hot days (T_{max} > 34.5 °C).

	Cool days (T_{max} <34.5°C)					Hot days (T_{max} >34.5°C)				
Diurnal period *microsite*	Selected	Available	X^2	Preferred / avoided	*Ei*	Selected	Available	X^2	Preferred / avoided	*Ei*
Morning										
exposed on ground	0.013	0.499	28	-	-0.95 ***	0.020	0.521	24	-	-0.93 ***
exposed off-ground	0.021	0.045	42	-	-0.36	0.019	0.041	20	-	-0.36
shaded on ground	0.010	0.042	28	-	-0.60 **	0.012	0.039	20	-	-0.51 **
shaded off-ground	0.020	0.018	42	+	0.04	0.020	0.016	24	+	0.09
Midday										
exposed on ground	0.018	0.567	6	-	-0.94 ***	0.013	0.566	6	-	-0.95 ***
exposed off-ground	0.026	0.023	20	+	0.06	0.012	0.027	6	-	-0.39
shaded on ground	0.015	0.012	35	+	0.10	0.017	0.011	12	+	0.20
shaded off-ground	0.027	0.015	42	+	0.29 **	0.032	0.016	42	+	0.34 *
Afternoon										
exposed on ground	0.011	0.524	18	-	-0.96 ***	0.021	0.598	15	-	-0.93 ***
exposed off-ground	0.018	0.073	42	-	-0.60	0.019	0.060	12	-	-0.51
shaded on ground	0.009	0.039	24	-	-0.63 **	0.010	0.017	15	-	-0.27
shaded off-ground	0.024	0.018	42	+	0.14	0.026	0.008	20	+	0.52 *

Table 3 Difference of *Ei* between hot and cool days showing whether each microsite was more preferred or avoided, 95 % confidence interval, Wilcoxon rank and p-values given per diurnal period (morning, midday and afternoon), exposure (exposed, shaded) and height category (on ground, off-ground) of each microsite.

Diurnal period *microsite*	Difference in *Ei* between cool and hot days	95% CI	Wilcoxon	p-value
Morning				
exposed on ground	0.02	-0.002 - 0.005	46250	0.33
exposed off-ground	0.00	-0.013 - 0.090	95628	0.14
shaded on ground	0.09	0.008 - 0.134	23422	**0.02***
shaded off-ground	0.06	-0.049 - 0.050	402790	0.98
Midday				
exposed on ground	-0.02	-0.011 - 0.002	2554.5	0.27
exposed off-ground	-0.45	-0.493 - 0.053	856	0.13
shaded on ground	0.10	-0.072 - 0.178	10288	0.38
shaded off-ground	0.05	0.000 - 0.000	239540	0.48
Afternoon				
exposed on ground	0.03	0.000 - 0.007	34490	**0.03***
exposed off-ground	0.08	-0.065 - 0.108	9491.5	0.58
shaded on ground	0.36	0.028 - 0.212	116910	**< 0.001*****
shaded off-ground	0.38	0.000 - 0.000	154050	**< 0.001*****

2.4.4. Behavioural patterns

Hornbill behavioural repertoires were more diverse on cool days compared to hot days (Shannon-Weiner H' cool days = 0.637; H' hot days = 0.564; Hutcheson's $t_{0.05(2),\ 2431}$ = -9.08, p < 0.001; Figure 8). This difference in diversity was mostly a result of increased inactivity at midday (cool days = 36.7 %; hot days = 51.2 %) and foraging behaviour in the morning (cool days = 33.9 %; hot days = 48.3 %) on hot days compared with cool days. In midday periods on hot days, the increased time that male hornbills spent inactive came at the expense of territorial and comfort behaviour, rather than foraging.

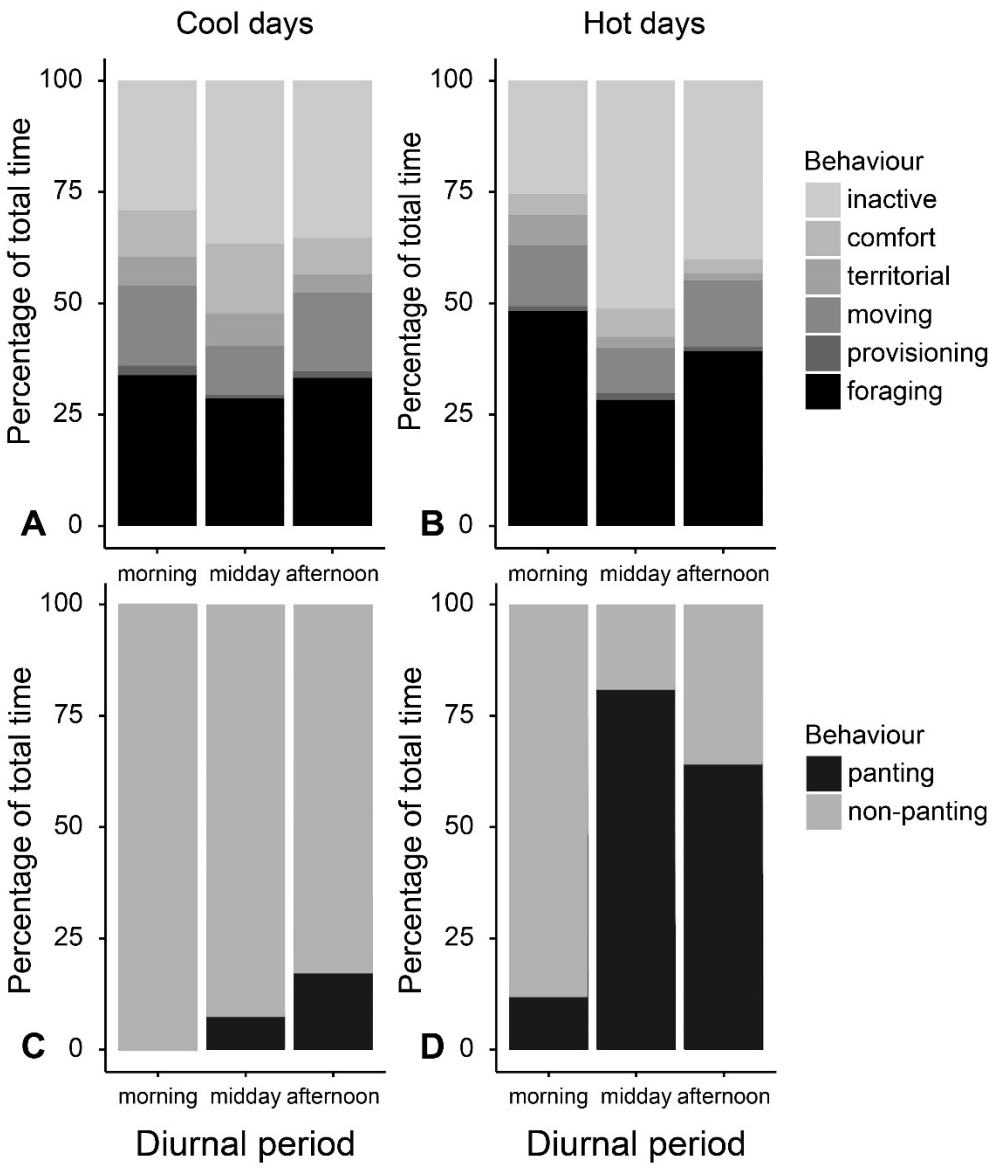

Figure 8 Percentage of time spent performing 'inactive', 'comfort', 'territorial', 'moving', 'provisioning' and 'foraging' behaviour per diurnal period on cool days (A; T_{max} < 34.5 °C) and hot days (B; T_{max} > 34.5 °C) by Southern Yellow-billed Hornbills. Percentage of time spent performing 'panting' and 'non-panting' behaviour per diurnal period on cool days (C; T_{max} < 34.5

°C) and hot days (D; T_{max} > 34.5 °C). Data were derived from 204 focal observations collected from 12 male hornbills.

2.4.5. Foraging effort

There were two competing models predicting foraging effort (proportion of time spent foraging) by the male hornbills. These included the variables 'T_a', 'chick age' and 'microsite' (Table 4).

Table 4 Top two models explaining effects on the proportion of time the male Southern Yellow-billed Hornbills spent foraging.

Model	df	logLik	AICc	ΔAICc	Model weight
Microsite + T_a	6	-264.25	540.9	0.00	0.488
Microsite + T_a + chick age	7	-263.66	541.9	0.97	0.300

Global model: microsite + T_a + chick age. Random term: Individual ID', 'focal ID' and 'season'.
n = 204 focal observations on 12 males.

The averaged parameter estimates of these two best-fit models indicated that the variable T_a had a significant positive impact on foraging effort (Figure 9) and male hornbills spent significantly less time foraging in exposed microsites off-ground and in shaded microsites on the ground. Chick age was present in the second competing model, but did not have a significant effect on foraging effort (Table 5).

Table 5 Factors affecting foraging effort of male Southern Yellow-billed Hornbills; estimates of effect sizes, standard error, z values and p values.

Variable	Estimate	Std. Error	Adjusted SE	z value	p value
T_a	0.03	0.01	0.01	2.165	0.030
Chick age	0.00	0.00	0.00	0.508	0.612
Microsite					
Exposed on ground	-0.23	0.31	0.31	0.744	0.457
Exposed off-ground	-3.85	0.38	0.38	10.096	< 0.001
Shaded on ground	-1.04	0.36	0.36	2.858	0.004
Shaded off-ground	-0.07	0.26	0.27	0.265	0.791

n = 204 focal observations on 12 males.

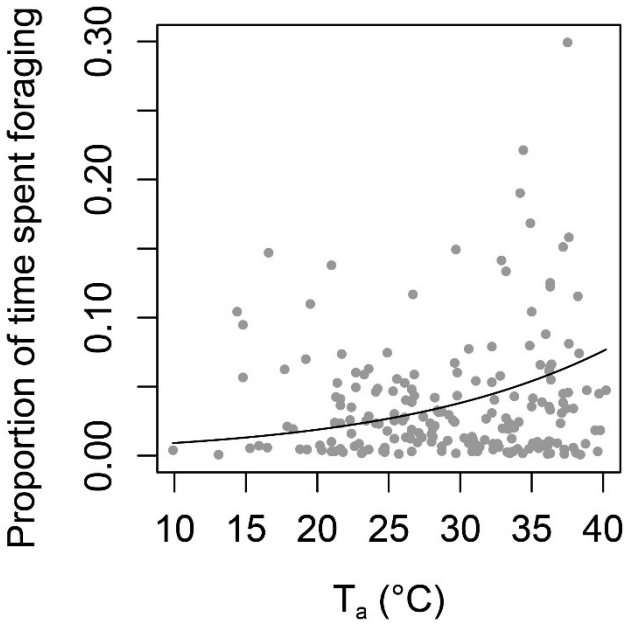

Figure 9 Proportion of time spent foraging as a function of T_a (°C) by male Southern Yellow-billed Hornbills. The black line represents the prediction of a model with a binomial error distribution that included the fixed variables 'T_a' and 'microsite'. 'Individual ID', 'focal ID' and 'season' were included as random factors. Data were derived from 204 focal observations on 12 males.

2.4.6. Foraging efficiency

There were two competing models that predicted foraging efficiency (prey captures per minute foraging) by the male hornbills. The best-fit model had a model weight of 0.707 and included the predictor variables 'microsite' and 'proportion of time spent panting' (Table 6). The second model contained only the predictor variable "microsite".

Table 6 Top two models explaining effects on foraging efficiency (prey captures per minute foraging) by male Southern Yellow-billed Hornbills.

Model	df	logLik	AICc	ΔAICc	Model weight
Microsite + proportion panting	7	-551.37	1117.0	0.00	0.707
Microsite	6	-553.29	1118.8	1.76	0.293

Global model: microsite + proportion panting . Random term: Individual ID', 'focal ID' and 'season'.
n = 35 focal observations on 7 males.

The averaged parameter estimates of these two best-fit models indicated that foraging efficiency decreased with the 'proportion of time spent panting' and when males were foraging in microsites off the ground. Foraging efficiency increased when males were foraging in microsites on the ground (Table 7).

Table 7 Factors affecting foraging efficiency of male Southern Yellow-billed Hornbills; estimates of effect sizes, standard error, z and p values.

Variable	Estimate	Std. Error	Adjusted SE	z value	p value
Proportion panting	-0.38	0.19	0.19	2.02	0.044
Microsite					
Exposed on ground	0.81	0.17	0.17	4.70	< 0.001
Exposed off-ground	-1.06	0.27	0.27	3.93	< 0.001
Shaded on ground	0.78	0.18	0.18	4.24	< 0.001
Shaded off-ground	-0.58	0.20	0.20	2.88	0.004

n = 35 focal observations on 7 males.

Within the same focal (therefore under the same T_a and presumably prey availability conditions) male hornbills caught on average 0.74 ± SD 0.62 prey items per minute foraging when they were not showing heat dissipation behaviour, but only 0.43 ± SD 0.51 prey items per minute foraging when they were panting: a reduction of 41.9 % (paired t-test, t = 2.78, p = 0.008; Figure 10).

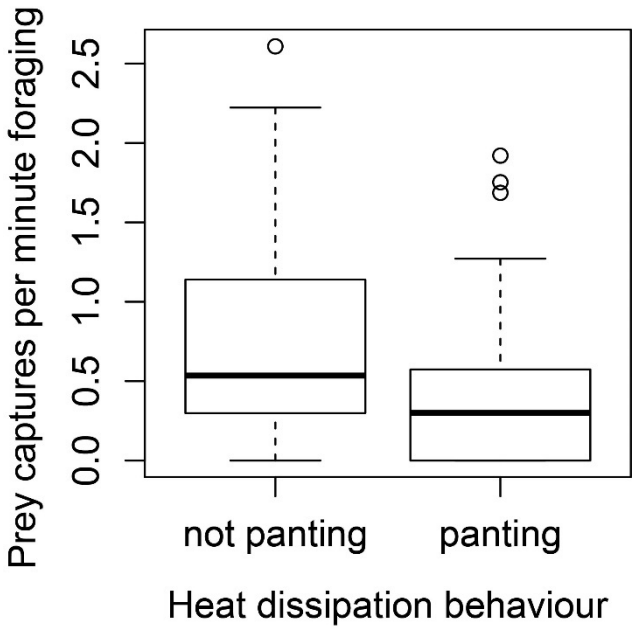

Figure 10 The interquartile range and median of prey captures per minute foraging by male Southern Yellow-billed Hornbills while 'not panting while foraging' and 'panting while foraging'. Data were derived from 35 focal observations on 7 males showing both panting and non panting behaviour while foraging during one focal observation.

2.4.7. Foraging success

Pseudoreplication in this zero-inflated poisson model was inevitable due to no random factors being fitted in this model. T_a had only a small effect on overall foraging success (prey captures

per 30-min focal) by the male hornbills (GLMM estimate = -0.10 ± 0.05, z = -2.23, p = 0.03; Figure 11). It is however unlikely that the increased foraging effort by male hornbills compensated for the decline in foraging efficiency during high T_a, hence the slight decrease observed in overall foraging success.

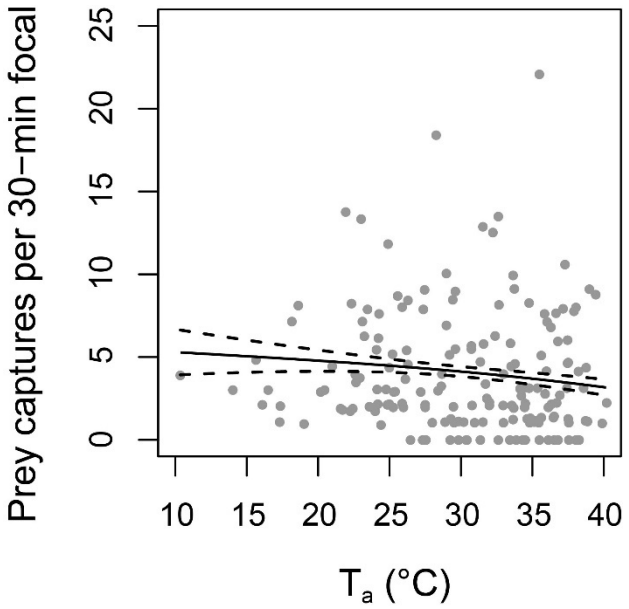

Figure 11 Prey items captured per focal observation as a function of T_a (°C) by male Southern Yellow-billed Hornbills. The black line represents the prediction of a model with a zero-inflated poisson error distribution that included the fixed variable 'T_a' and the dashed lines represent the 95 % CI. Data were derived from 204 observations on 12 males.

2.5 Discussion

During hot periods, male Southern Yellow-billed Hornbills struggled to maintain their foraging intake, despite increasing the proportion of time they spent foraging. This is due to a reduction in foraging efficiency at high T_a, which in turn seemed to be associated with a preference for cooler microsites that were sub-optimal for foraging, and the reduced prey capture rate while panting. The birds in this study were breeding. Therefore, in addition to supplying their own foraging demand, they were solely responsible for provisioning females and nestlings sealed within their nests. During hot weather, they likely faced increased need for water-rich prey items to match their own thermoregulatory demands (evidenced by increasing rates of panting, promoting evaporative water loss, as T_a increased) and those of their mate and nestlings. It seems unlikely that this increased demand for water-rich prey on hot days could be met by the male hornbills given their inability to increase their foraging intake.

Evaporative heat loss in hornbills via panting is an important mechanism of heat dissipation and is performed at T_as as low as 23.5 °C. Heat dissipation behaviour in Southern Yellow-

billed Hornbills was positively correlated with T_a and at T_a > 34.5 °C the birds spent more than half of their time panting. This form of thermoregulatory behaviour carries the physiological cost of water loss via evaporation from the body (Tieleman et al., 2003). Hornbills do not drink water and the only source of water intake is via food items (Kemp, 1976). On hot days, this creates conflicts between hyperthermia avoidance (inactive behaviour = low metabolic heat production) and dehydration avoidance (actively foraging to obtain water rich food items) (Smit et al., 2016). Since males were observed to spend more time inactive on hot days and foraging efficiency was reduced, it is likely that hot weather negatively affected their hydration state. Birds can quickly rehydrate when access to food items improves (Leberg et al., 1996). However, for male hornbills the risk of dehydration could become problematic if they experience increasing numbers of consecutive days with high T_a, for example during heat waves.

Male hornbills lowered the physiological impact of high T_a by selecting cooler microsites, presumably to reduce their need for evaporative water loss. Selection of microsites with a low thermal load may lower the impact of the thermal environment on animals. Therefore the availability and usage of thermal refugia could reveal important information regarding the vulnerability of species to climate warming (Hall et al., 2016) and moreover, could have important implications for conserving threatened species in very hot areas. Mean T_e in the hornbill territories differed by as much as 12.8 °C between exposed microsites on the ground and shaded microsites off-ground at the hottest time of day (14h00). Studies ignoring the effects of T_e are therefore likely to underestimate the effects of variation in thermal load on animals (Camacho et al., 2015). For example, based on T_a obtained from the weather station I could have concluded that the hornbills avoided open ground areas due to predation risk, as is seen in other birds (Cresswell, 2008). Data on thermal conditions provide the important alternative hypothesis that hornbills were avoiding these microsites due to the high T_es which exceeded the panting threshold temperature between 8h00 and 7h00 on an average day. Both predator avoidance and heat load avoidance behaviours are plausible assumptions to explain the preference for hornbill males to select microsites off the ground.

Thermoregulatory behaviour, including microsite selection and heat dissipation behaviours (e.g., panting) can come at the cost of missed opportunities (du Plessis et al., 2012; Cunningham et al., 2015; Edwards et al., 2015). Selection of cool microsites can mitigate thermoregulatory demands in hot environments, but can also incur costs of missed opportunities which can affect fitness (Edwards et al., 2015). The hornbills in this study had the highest prey capture rates in exposed microsites on the ground. On hot afternoons,

however, they preferred shaded microsites off the ground, which were sub-optimal locations for foraging. Thermoregulatory behaviour in response to hot weather events has the potential to limit foraging opportunities (van Beest et al., 2012) and the cost of high temperatures on species is often expressed as reductions in foraging success and activity levels (Cerdá et al., 1998; Owen-Smith, 1998; Nowicki et al., 2012; Edwards et al., 2015; Abadi et al., 2016). In arid environments for example, foraging success of Southern Fiscals (*Lanius collaris*) declined by ~ 50 % when they changed their hunting strategy from sunny to shaded perches (Cunningham et al., 2015) and in Southern Pied Babblers (*Turdoides bicolor*) the cost of panting behaviour while foraging caused foraging efficiency to reduce by as much as 74 % (du Plessis et al., 2012). In this study, I found that foraging efficiency by male hornbills declined with an increased proportion of time spent panting and selection of cooler off-ground microsites. If the frequency of hot days increases in the future, male hornbills might spend an increasing amount of time in shaded microsites off the ground to reduce thermoregulatory costs, while simultaneously facing missed foraging opportunities.

Male hornbills adjusted their time-activity budgets on hot days compared to cool days, specifically by increasing their time spent foraging during the cooler morning and afternoon on hot days; and increasing time spent inactive during the heat of the day. They were therefore able, to some extent, to make up for the missed foraging opportunities caused by behavioural thermoregulatory demands (panting and microsite use changes) at midday on hot days. This finding is similar to that of Carroll et al. (2015), where Northern Bobwhites (*Colinus virginianus*) prioritised foraging in the early hours on hot days presumably in anticipation of extreme temperatures. I suggest that animals, including hornbills, can anticipate hot weather events and to a certain extent counteract compromised foraging conditions via adjustment of time-activity budgets.

Changes in time-activity budgets may still entail costs. In this study, I observed that male hornbills sacrificed territorial and comfort (preening) behaviours (rather than foraging) in order to increase time spent inactive on hot days. The territorial behaviours that I observed were primarily interactions with other species (mobbing) and calling in the context of territorial behaviour. Territorial calling is associated with increased respiratory water loss, as was confirmed in a study on Willow Warblers (*Phylloscopus trochilus*) (Ward and Slater, 2005). Male hornbills potentially reduced territorial behaviour in exposed microsites on hot days to avoid water lost through territorial calling. This finding suggests that territorial behaviour of hornbills could be compromised as climate warming continues. Hornbills also curtailed comfort behaviours, including preening, on hot days. Reduced preening behaviour by Hoopoe-larks

(*Alaemon alaudipes*) in the Arabian desert in response to high T_a was predicted to lower both flight performance and thermoregulatory properties of the feathers (Tieleman and Williams, 2002b), and this may also be the case in hornbills. Changes in behavioural patterns observed in the male hornbills were closely linked to T_a and time of day, but given the potential consequences mentioned above; these behavioural changes may not reflect hornbill resilience to future warming scenarios.

2.6 Conclusions

The capacity for species to use behavioural thermoregulation is proposed to increase their resilience to future warming scenarios (Huey et al., 2012). However, in this study, changes in time-activity budgets, microsite preference, and the use of panting behaviour for evaporative cooling, were all accompanied by costs. Thermoregulatory trade-offs caused a reduction in foraging efficiency when male hornbills favoured shaded off-ground microsites and when they performed panting behaviour while foraging during periods of high T_a. Furthermore, the fact that hornbill males already spent most of their time in the coolest microsites (shaded microsites off the ground) on hot days, suggests that their current habitat might not provide sufficient optimal thermal refugia when T_as rise in the future. Changes in behavioural patterns in response to hot days led to decreased territorial calling as well as negligence of feather maintenance. The increased time spent foraging as T_as increased did not make up for the reduced foraging efficiency and therefore overall foraging success was stable or decreased with increasing T_a. Given that water losses are higher on hot days (as shown by an increased proportion of time spent engaged in panting), this decrease in foraging success will likely negatively impact male, female and chick hydration states and limit their capacity for evaporative cooling. Reduced water and energy intake on hot days can also be predicted to negatively influence the ability to maintain M_b in adults and growth rates in chicks (addressed in Chapters 3 and 4). It therefore seems unlikely that the behavioural thermoregulatory responses of the hornbills in this study will be sufficient to buffer them against the increasing frequency and duration of hot weather events under climate change.

CHAPTER 3 THE COSTS AND CONSEQUENCES OF THERMAL TRADE-OFFS IN A SINGLE PROVISIONER

3.1 Abstract

Male Southern Yellow-billed Hornbills (*Tockus leucomelas*) are single provisioners for part of the nesting season. During this time, they need to share foraging yield between themselves and the female and chicks inside the nest. Hornbills do not drink, but obtain all water through their diet. On days when air temperatures (T_as) are high, they dissipate heat via elevated rates of evaporative water loss, which results in higher food demands. However, in the previous chapter, I concluded that the males' foraging intake was not increased on hot days, despite increased foraging effort. Given the elevated water requirements of both males and females and chicks in the nest on hot days, in this chapter I assess whether males make trade-offs between nest provisioning and their own food intake as T_as increases. The aim is to understand the effect of high daily T_a on prey allocation decisions, and the consequences for nest provisioning and male body mass (M_b). Prey allocation decisions were recorded with each successful foraging attempt during behavioural observations of breeding male hornbills. Provisioning rates were quantified using cameras placed at the nest, and M_b of the males was recorded with every nest visit using a perch scale installed at the nest box.

I found that male hornbills provisioned larger prey items to the nest and consumed smaller items themselves, irrespective of T_a. Heavier males allocated proportionately fewer prey items to the nest (therefore making fewer provisioning trips) than lighter males. As T_a increased the biomass caught decreased, resulting in a lower biomass provisioned to the nest overall. The negative effect of daily maximum air temperature (T_{max}) on provisioning rate and biomass provisioned was similar when males were single provisioners and when both adults were provisioning the nestlings. That is, females were unable to compensate for reduction in provisioning effort by males at high T_a. Males were unable to maintain M_b on days when T_{max} exceeded 37.9 °C. Daily mean M_b of the males was affected most strongly by T_{max} of the preceding day, chick age and initial male M_b. Failure of nesting attempts was correlated with a high mean T_{max} during the nestling period which resulted in males losing more mass over a shorter period. During hot nesting periods, fathers provisioned and consumed less prey overall, suffering increased mass loss and reduced nest success: paying the cost of reproduction without any return.

3.2 Introduction

Recent changes in environmental temperatures and rainfall patterns have increased the need for endotherms to migrate to more suitable habitats or to phenotypically adjust to the changed climatic conditions (Fuller et al., 2010; Boyles et al., 2011; Khaliq et al., 2014). Periods of extreme high air temperatures (T_a) in Australia, for instance, have on occasion led to mass mortalities among birds (McKechnie and Wolf, 2010), but the sublethal effects of high daily T_as can also lead to major impacts on fitness and reproductive success (McKechnie et al., 2012). These sublethal effects can be measured in terms of diurnal body mass (M_b) changes (measured within-individuals as a proxy for changes in body condition) in response to environmental changes (Blaustein et al., 2010). In the Southern Pied Babbler (*Turdoides bicolor*), a desert specialist, T_as exceeding 35.5 °C resulted in the birds being unable to regain mass lost overnight (du Plessis et al., 2012). A long-term study of White-plumed honeyeaters (*Ptilotula penicillatus*) revealed that consecutive days of high T_a and low rainfall lead to a reduction in body condition and a decline in survival rate (Gardner et al., 2016). The effect of high T_as on body condition can affect parental decisions and even lead to nest abandonment (Amat and Masero, 2004). In hornbills, abandonment could have further repercussions since the females are confined within the nest for the first part of the breeding period, during which they undergo a flightless moult. During this time, they are as dependent on the male's care as the chicks are (Chapter 1). If the males were to abandon the nest due to the impacts of high heat loads before the females regrow their primary feathers, they would be unable to fly, forage or escape predators outside of the nest and would likely not survive.

Many desert birds, including Southern Yellow-billed Hornbills (*Tockus leucomelas*) living in arid environments, obtain all their water via their food intake and do not rely on free-standing water (Maclean, 1984). When T_a approaches or exceeds T_b, hornbills, like other birds, defend T_b within a tolerable range via evaporative cooling: a costly mechanism in an environment where water is scarce (Smit et al., 2013). Southern Yellow-billed Hornbills are opportunistic foragers, with a diet typically comprising invertebrates, reptiles, fruit and also small mammals and birds (Kemp, 1995). Larger prey items have a higher water content and therefore form an important source of water (Tremblay et al., 2005). On days when T_as are high, there will be a high food demand from the nest in order to replenish the females and the nestlings' water balance, this is in addition to the need for the provisioning males to replace their own body water. For parents with a provisioning task, this can lead to trade-offs between foraging and the need to reduce activity and seek shaded microsites (lowering both evaporative water loss and metabolic heat production; Chapter 2) (Dawson et al., 2005; Stein et al., 2009).

It is hypothesised that large prey items with high energy content are worth spending the increased energy of delivery to the nest (McNamara and Houston, 1997). Hornbill males are central place foragers and single-prey loaders during the nesting period, meaning that they carry one food item at a time and are likely to adjust travelling distance according to prey size (Orians and Pearson, 1979). However, during the hot periods of day, prey items like invertebrates, reptiles and small mammals become less active and hide in thermal refuges, becoming more difficult to detect by foraging birds. For example, a study on the thermal tolerance of a population of desert tenebrionid beetles (*Gyriosomus spp.*) in Chile showed that the beetles reduced activity during extreme low and extreme high T_as of day (Vidal et al., 2011). Two species of tenebrionid beetle (*Physadesmia globosa* and *Onymacris rugatipennis*) in the Namib desert avoid the heat by burying in the sand, a form of behavioural thermoregulation that effectively reduces their T_b (Ward and Seely, 1996) but which also makes them less available to foraging birds. This suggests that increased foraging effort by birds in deserts will be required to obtain certain prey items during hot periods. During the hottest time of day the hornbill males therefore face major challenges: 1) body water pools of the males as well as the females and chicks in the nest need to be replenished via high-water content prey items during periods when evaporative water losses are elevated and 2) larger prey items are more difficult to find during hot periods and therefore require increased foraging effort (see Chapter 2). Smaller prey items will not justify the effort of the males to fly the distance to provision the nest as males must also seek to reduce energy spent on foraging activities and to reduce metabolic heat production during flight and foraging. Provisioning males need to assess whether the fitness benefit (reproduction) of provisioning the item outweighs the fitness cost (their own survival) of delivering the item.

In birds, the provisioning of food items to the nest is dependent on the foraging success of the parents and the allocation decisions they make with every successfully caught prey item. In Chapter 2, I concluded that in this study population of hornbills, males are unable to increase the amount of prey captured when T_a increases. Therefore, on hot days, males need to make critical decisions about allocating prey to themselves *versus* the females and chicks in the nest. Several studies have described determinants of provisioning rate to chicks, ranging from changes in food availability (O'Neill Goodbred and Holmes, 1996; Smithers et al., 2003; Morrison et al., 2016), to changes in microsite preference by the parent (Cunningham et al., 2015). When food is readily available, parents should provision the nest in accordance to the needs and the number of chicks (Davis et al., 1999; Ochi et al., 2009). The state of parental body condition however, can determine provisioning effort, resulting in adults feeding less to the chicks and consuming more food themselves as their M_b reaches a lower limit

(Weimerskirch et al., 1997; Weimerskirch et al., 2000). The increased thermoregulatory cost limiting foraging success in this population of hornbills on hot days (see Chapter 2) could therefore negatively affect the females and chicks in the nest, as well as the males themselves. For example, one possible effect of high T_a could be that during the hot periods of day, males opt to consume small prey items and revert to provisioning the nest only when larger prey items can be caught as T_as cool down towards sunset.

In this chapter I focused on the provisioning rate and allocation of dietary items by male hornbills and how their decisions are influenced by T_a as well as their own M_b. I quantified size and number of prey items consumed or provisioned, nest provisioning rate, biomass provisioned and diurnal M_b change of the males. I hypothesised that allocation of prey items would be dependent on the size of the captured prey item and current male M_b, as a result of thermoregulatory trade-offs associated with T_a. Furthermore, I hypothesised that provisioning rate and biomass provisioned would be influenced by chick age and brood size as well as T_a, since dietary demand increases with chick growth but also with thermoregulatory requirements and thermal load experienced by the nestlings (transition from poikilothermy to homeothermy during chick development (Whittow and Tazawa, 1991). I predicted that male diurnal M_b change (amount of mass gained between dawn and dusk; measured at the scale of days) would be negatively correlated with maximum air temperature (T_{max}) and that daily mean M_b of the males (average of all mass measurements during a day) would be influenced by T_{max} of the previous day, their initial M_b at the start of breeding and the length of time they have spent caring for the chicks (i.e., chick age). Finally, I assessed how high T_as affected nesting success and how length of nesting period and daily male M_b loss during the nesting period differed between nests that successfully fledged chicks and nests that failed to fledge any chicks.

3.3 Methods

3.3.1. Study site and population

I observed semi-habituated, male Southern Yellow-billed Hornbills at the Kuruman River Reserve (26°85’ S, 21°49’ E). Observations took place in the austral summers during the hornbill’s breeding season, which coincides with the highest annual temperatures. All data were collected from breeding males during the nestling period between hatching of the first chick and fledging of the last chick. For a full description of the study site and population see Chapter 1.

3.3.2. Behavioural observations

A total of 204 thirty-minute behavioural observations (hereafter called ‘focals’) were collected from twelve breeding male hornbills during three diurnal periods (sunrise – 10h59, 11h00 – 14h59 and 15h00 – sunset) on a total of 86 days across three breeding seasons between October and March from 2012 to 2015, using Cybertracker software (CyberTracker 3.372) (for details of focal protocols, see Chapter 2). As part of the focal data collection, information on foraging behaviour was collected. Foraging behaviour was identified by ‘searching’ behaviour by the focal individual followed by a prey item escaping, not being found or successfully being caught by the male. Each successfully caught prey item was identified to Order level and the number of items, the size of each item and the allocation of the prey item was recorded. The allocation of prey items was recorded as ‘self’ if the males consumed the item, as ‘nest’ if the males provisioned the item to the nest or as ‘unknown’ if the outcome was uncertain. Both the proportional allocation of prey items and the proportional allocation of biomass (see below for information on calculation of biomass) were analysed per focal observation. Length of focals was on average 29.5 ± SD 5.3 minutes, with a range of 16.6 – 39.9 minutes. Foraging success data were therefore standardised to 30-min focals by dividing the total of prey items and the total of biomass by the actual number of minutes of the focal observation and were multiplied by 30. Sample size of focals with information on prey allocation (n = 149) was lower than the total number of focal observations collected (n = 204) due to exclusion of focals where no prey items were caught successfully or where allocation of items was unknown. Sample size of focals for biomass allocation (n = 104) was lower than those of prey allocation due to missed records of prey item identification.

3.3.3. Relationship between provisioning rate and biomass delivered

Biomass per prey item type was calculated as the average live mass of at least five specimens of each prey taxa, drawn from a reference collection (Table 1). Prey items for this reference collection were collected during summer between 2012 and 2015 and match the spectrum of the hornbill’s diet as observed from the focal observations. Prey item sizes observed during focal observations were recorded as an estimate relative to beak size and recorded as categories: 'tiny', '< 1/3 of the beak’,’1/3 of the beak’, '2/3 of the beak', 'same size as the beak' and '> beak'. Some items were unavoidably missing from the reference collection due to difficulty of catching these. The biomass of the missing prey items was estimated from a prey reference collection for meerkats (*Suricata suricatta*) at the Kuruman River Reserve (unpubl. data T. Chalikonda).

Table 1 Prey items captured by male Southern Yellow-billed Hornbills as recorded during focal observations and from nest cameras. Classified by order, common name (as noted during focal data collection), size class and average wet biomass of the prey item (g). The avian eggs that were observed in the diet were acquired from Southern Pied Babbler (*Turdoides bicolor*), Fork-tailed Drongo (*Dicrurus adsimilis*) White-browed Sparrow-Weaver (*Plocepasser mahali*) and Cape Turtle Dove (*Streptopelia capicola*) nests. The mass estimate of the avian egg is taken from an average of two Southern Pied Babbler eggs and three Fork-tailed Drongo eggs acquired from abandoned nests (< 2 days after abandonment) at the study site.

Taxonomic group	Common name	Size class	Wet biomass (g)
Hymenoptera	ant	tiny	0.0
Isoptera	termite	tiny	0.0
Mantodea	mantis	< 1/3 of the beak	0.2
Diptera	fly	< 1/3 of the beak	0.3
Lepidoptera	caterpillar	< 1/3 of the beak	0.3
Orthoptera	grashopper	< 1/3 of the beak	0.3
Lepidoptera	moth	< 1/3 of the beak	0.4
Lepidoptera	butterfly	< 1/3 of the beak	0.5
Malvaceae	grewia fruit	< 1/3 of the beak	0.5
Arachnida	spider	1/3 of the beak	0.6
Cicadidae	cicada	1/3 of the beak	0.7
Coleoptera	beetle	1/3 of the beak	0.8
Scorpiones	scorpion	2/3 of the beak	0.9
Solifugae	solifuge	2/3 of the beak	1.6
Spirostreptida	millipede	2/3 of the beak	1.6
Avian egg	egg	2/3 of the beak	1.8
Annelida	worm	2/3 of the beak	2.7
Scincidae	skink	same size as the beak	3.0
Chiroptera	bat	> beak	4.1
Squamata	snake	> beak	4.6
Columbiformes	chick	> beak	5.2
Rodentia	small mammal	> beak	5.3

Although correlated, daily provisioning rate was not a good proxy for daily biomass delivered to the nest (relationship between the two variables: R^2 = 0.57; LMM estimate: 0.37 ± 0.03, t = 11.53, p < 0.001; Figure 1) and therefore analyses of both variables are presented in this chapter.

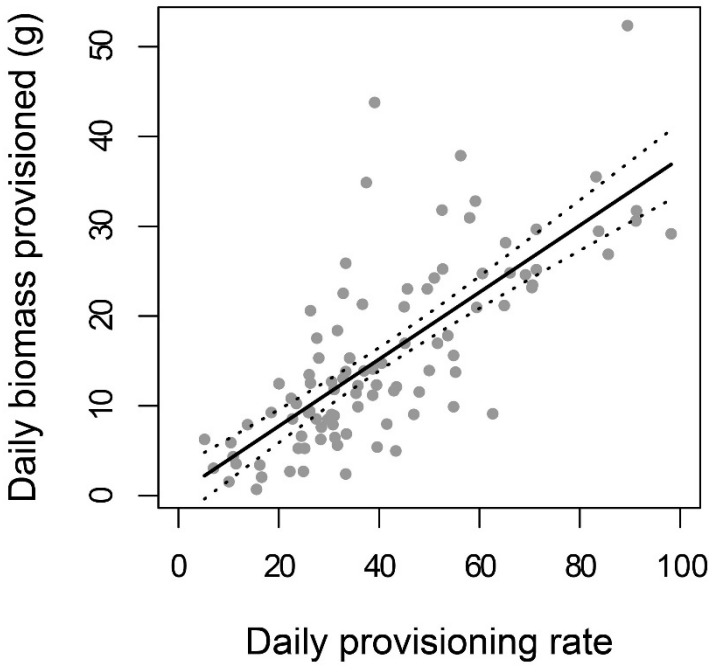

Figure 1 Daily biomass provisioned as a function of daily provisioning rate by male Southern Yellow-billed Hornbills (R^2 = 0.57), showing a strong but noisy relationship which suggests provisioning rate is not a good proxy for biomass delivered to the nest.

3.3.4. Provisioning assessment

Daily provisioning rate and biomass provisioned were collected at nests during one breeding season (2014 – 2015) on a total of 99 days from seven different nests. Motion triggered cameras (BTC-5, Browning, U.S.A) set to record a 30-sec video clip with each trigger were used to assess provisioning rate. The cameras were positioned 2 - 3 metres in front of the hornbill nests from sunrise until sunset. The aim was to assess provisioning rates on days with a range of different T_{max} and different chick ages. Provisioning assessment was done during 25 'cool' days (T_{max} < 34.5 °C; chick age categories: 0 – 10 days (n = 9), 11 – 30 days (n = 9) and 31 days and older chicks (n = 7) and 74 'hot' days (T_{max} > 34.5 °C; chick age categories: 0 – 10 days (n = 7), 11 – 30 days (n = 41) and 31 days and older chicks (n = 26). Provisioning assessment included the period after female departure from the nest, when both male and female provisioned the nest.

The reliability of data from the motion triggered cameras was assessed by setting up a motion triggered camera and a continuous-recording HD video camera (HDR-XR160E, Sony, Japan) simultaneously on eight days at three different nests with chicks from all three age categories. I compared the number of provisioning events captured by the motion-triggered cameras with those recorded during the same day at the same nest by the HD-cameras. The time stamp of a provisioning visit by the bird was compared between the two camera types and revealed that

the motion triggered camera managed to capture 99.3 % of all the visits to the nest. Provisioning rates were calculated from the total number of provisions on a day divided by the time in hours that the nest camera had been operative on that day and then multiplied by 12 to standardise provisioning rate to a 12-hour day. Observation days where the camera had been operative for less than ten hours were discarded, this usually occurred as a result of battery failure (n = 45). The age of the chicks was taken as the date of hatch of the first chick (day of hatch = 0), and the number of chicks in the nest was checked and recorded on each day the camera was placed.

3.3.5. Collection of body mass data

During the breeding season, M_b of breeding male hornbills was recorded using perch scales (B0.6U, Axis, Ecotone, Poland) mounted at nest entrances (n = 14 nest boxes and n = 2 natural cavities). Each perch scale consisted of a small (10 cm) tree branch attached to a load cell which was mounted horizontally (confirmed using a spirit level) on the side of the nest box or tree trunk (natural cavities), using a metal bracket to ensure the load cell did not touch the nest box / trunk. The load cell was connected to a digital scale which stored the mass data and date-timestamp on an external USB flash drive. The scale was powered by a 12V lead acid battery. The branch affixed to the load cell was placed as such that it provided the most logical perch from which to provision the prey item to the nest entrance (Figure 2). The M_b data provided an estimate of male M_b across the nesting period, as well as providing information on diurnal M_b gain in relation to daily T_{max}. Morning and evening masses were taken as the earliest (within half an hour before to half an hour after sunrise: mean 5h43, range: 5h36 – 5h53) and latest (within half an hour before to half an hour after sunset: mean 19h26, range 19h19 – 19h30, calculated from the local latitude and sun declination) M_b record whereby the male sat correctly on the perch scale. The video footage was examined to establish bird identity using colour ring combinations and to ensure the bird correctly used the perch scale, i.e., both feet on the perch, and not touching any other parts of the nest box or the load cell itself. Total diurnal M_b gain was expressed as a percentage of the morning M_b and corrected for time elapsed between the morning and the evening measurement following du Plessis et al. (2012):

$$\Delta M_b = 100[(w2 - w1)/\, w1] \,/\, [\,\Delta t/12]$$

The diurnal percentage M_b gain was calculated by taking the difference of morning M_b (w1) and evening M_b (w2) and by incorporating the time difference between the morning time value (t1) and evening value (t2), generating the number of hours between t1 and t2 = Δt (equation from du Plessis et al. (2012). Perch scale data collection coincided with provisioning rate and

focal data collection at the same nest and on the same day. Due to battery failures of scales and incorrect use of the perch by the bird the sample size for bird M_b is lower than for provisioning and observational data: with a final sample size of 122 days M_b collection from ten different males during 14 breeding attempts across three breeding seasons.

Figure 2 A male Southern Yellow-billed Hornbill (individual ID: GMOR of nest ID: LEA05) correctly using a perch scale mounted to a nest box. Note both feet on the perch and no body parts touching the nest box or other parts of the scale, ensuring a correct M_b reading (photo credit: Dean Portelli).

3.3.6. Statistical analyses

All analyses were conducted in the R statistical environment using R Studio interface (R Development Core Team, 2016). General linear mixed models (GLMM) and linear mixed models (LMM) were computed using the lme4 package (Bates et al., 2015) and the MuMin package was used for model selection and averaging (Bartoń, 2015). I constructed a global model that consisted of all the variables I hypothesised to have an effect on the response variable. Best-fit models were chosen based on comparison of the Akaike Information Criterion corrected for small sample size (AICc) between all possible nested models within the global models, using the "dredge" function in MuMin. Goodness of fit to model assumptions were assessed with residual plots, and all models with ΔAICc < 2 were retained. I present model averaged estimation of effect sizes, standard errors and p-values when the set of best-fit

models (ΔAICc < 2) contained more than one model. Random terms were included in each model to account for non-independence due to repeated measures of individuals within seasons. Prior to fitting global models, linear regression was used to check for collinearity of the predictor variables and correlated variables were never included in the same model. All analyses include data collected during the period between hatching of the first chick and fledging of the last chick. P-values < 0.05 were taken as statistically significant and mean estimates are reported ± 1 standard error (SE) unless otherwise stated.

Biomass captured per focal

Biomass captured by males during 30-min focal observations was analysed as a LMM with a Gaussian error distribution including the variables T_a, chick age and brood size with individual identity nested within season included as a random term. Time of day was correlated with T_a and therefore not included in the model. Data were derived from 104 focal observations during 11 nesting attempts by 8 males across 3 seasons.

Proportional allocation of prey items on cool and hot days

Proportional allocation (self versus nest) of prey items per prey size category were analysed as a function of cool versus hot days to assess whether the size distribution caught matched the size distribution allocated. Days were classified as cool or hot based on whether daily T_{max} was below or above the panting threshold temperature (34.5 °C) at which individuals spent half of their time performing heat dissipation behaviour (identified in Chapter 2); to facilitate the analysis. The distribution of prey item sizes was compared with Pearson's chi-squared test between allocation (nest versus self) and T_{max} category (cool versus hot days). Data were derived from 104 focal observations during 11 nesting attempts by 8 males across 3 seasons.

Prey allocation to nest versus self from focal observations

Allocation of prey items was derived from the focal observations during the period from chick hatch to chick fledge. A combined vector of 'count of prey provisioned to the nest during a focal' versus 'count of prey consumed by the males during a focal' with a binomial error distribution was modelled as a function of the predictor variables T_a, daily mean male M_b (calculated as the daily average of all M_b measurements from the perch scale at the male's nest, where it could be ascertained the males sat correctly on the scale), brood size and chick age. Individual identity nested within season was included as a random term. Sample size was 149 focal observations during 11 nesting attempts by 8 males across 3 seasons.

Biomass allocation to nest versus self from focal observations

Allocation of biomass was derived from the focal observations and calculated as biomass allocated during the period from chick hatch to chick fledge. A combined vector of 'biomass provisioned to the nest during a focal' versus 'biomass consumed by the male during a focal' with a binomial error distribution was modelled as a function of the predictor variables T_a, brood size and chick age. Individual identity was included as a random factor. Sample size for 'biomass allocated' is lower than 'count of prey allocated' since not all prey items were identifiable. For this reason, the variable daily mean male M_b was not included in the analysis as it would have lowered sample size to 50 focal observations. Sample size was 104 focal observations on 11 nesting attempts by 8 males across 3 seasons.

Daily provisioning rate from nest cameras

Provisioning rates were derived from nest camera data and analysed separately for the period during which male hornbills were single provisioners and the period after female hornbills left the nest, but before the chicks fledged, when males and females shared provisioning. Daily provisioning rate was analysed using a GLMM with a Poisson error structure (as these were count data) and a log-link function including the predictor variables T_{max}, chick age and brood size. Individual identity was included as a random term for male single provisioning analysis (n = 45 observations on five males) and individual identity nested in nest identity was included as a random term for male and female shared provisioning (n = 54 observations on seven hornbill pairs).

Daily biomass provisioned from nest cameras

Nest provisioning was furthermore calculated as the daily biomass provisioned (g) and this was modelled as a LMM with a Gaussian error structure again with separate models for male single provisioning and male and female shared provisioning. A Gaussian error structure was used because the data were sums of daily biomass delivered to the nest and the datasets were normally distributed. The predictor variables included in the global models were T_{max}, brood size and chick age. Only two nests had more than one chick when male and female shared provisioning, therefore brood size was excluded as a predictor variable from the shared provisioning analysis. Individual identity was included as a random term for male single provisioning analysis (n = 45 observations on five males) and individual identity nested in nest identity was included as a random term for male and female shared provisioning (n = 54 observations on seven hornbill pairs).

Male body mass

Diurnal M_b change of the male hornbills was analysed as a LMM with a Gaussian error structure including the predictor variables T_{max}, chick age and brood size with individual identity nested in season included as a random term. Diurnal M_b change was calculated from 73 days during ten nesting attempts of seven males from which I had a reliable M_b record at sunrise and sunset.

Daily mean M_b (average of all reliable M_b measurements per male between dawn and dusk each day) of the males during the nesting period was analysed as a LMM with a Gaussian error structure including the predictor variables chick age, initial male M_b when chicks hatched and T_{max} of the day prior to M_b measurement. Individual identity nested in season was included as a random term. Daily mean male M_b data were derived from 122 days during 14 nesting attempts of ten males between chick hatch and chick fledge.

Nesting success

Mean T_{max} during the nesting period (calculated as the mean of daily T_{max} for the nestling period between hatching of the first chick and fledging of the last chick per nest), length of the nestling period, initial male M_b at chick hatch, final M_b at chick fledge and daily mean male M_b loss during the nestling period were compared between successful and failed nests with a Student's t-test. Data were derived from 7 males during 8 nesting attempts (successful nests: n = 4; failed nests: n = 4) from which I had collected M_b within 8 days after chick hatch and within 9 days before chick fledge.

3.4 Results

3.4.1. Biomass captured per focal

The best-fit model explaining the variation in total biomass of prey captured per 30-min focal observation contained only T_a as the predictor variable and had a model weight of 0.738. There were no competing models within two ΔAICc points. As T_a increased, the biomass of prey captured per 30-min focal observation was reduced (LMM estimate: -0.10 ± 0.03, t = -3.87, p = 0.002) (Figure 3).

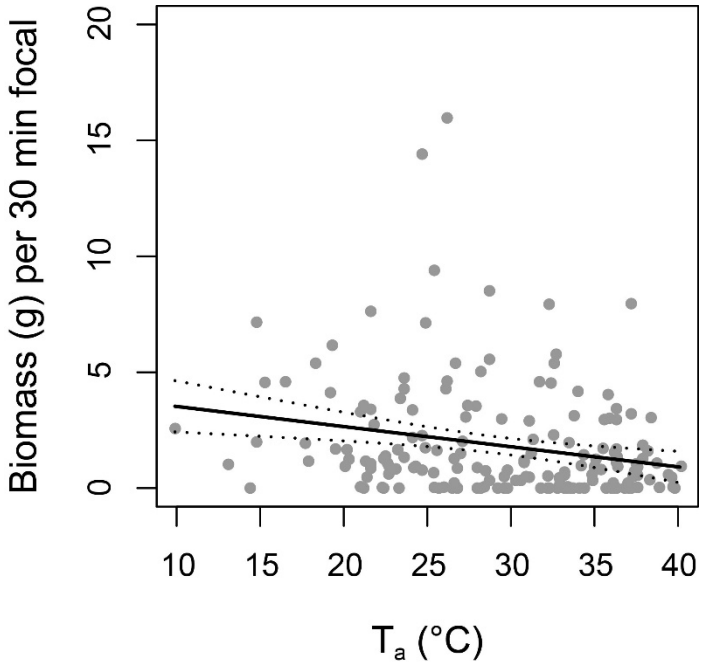

Figure 3. Biomass captured (g) per 30-min focal as a function of T_a (°C) by the male Southern Yellow-billed Hornbill. The black line represents the model predictions with T_a as a fixed variable (chick age and brood size had no effect and were excluded from this model) and individual ID nested within season was used as a random effect. The dotted lines represent the 95 % confidence intervals. Data were derived from 104 focal observations during 11 nesting attempts of 8 males.

3.4.2. Proportional allocation of prey items on cool and hot days

On both cool and hot days, the size distribution of the prey items provisioned to the nest was significantly different from the size distribution of prey items consumed by the males (Pearson's chi-squared tests: cool days to nest versus cool days to self $X^2_{0.05(5),\ 11.07} = 24.78$, $p < 0.001$; hot days to nest versus hot days to self $X^2_{0.05(4),\ 9.48} = 58.37$, $p < 0.001$). On both hot and cool days, this pattern was associated with the males generally consuming smaller prey items and provisioning larger prey items. For example, tiny prey items were rarely provisioned to the nest (4.8 % of total prey provisioned on cool days and 4.0 % on hot days), but were mostly consumed by the males themselves (32.7 % of total prey consumed by the males on cool days and 48.6 % on hot days; Figure 4). In addition, there was no difference in the size distribution of the prey items eaten by the males on cool days compared to hot days (Pearson's chi-squared test; cool days to self, versus hot days to self: $X^2_{0.05(3),\ 7.82} = 6.12$, $p = 0.11$). Despite this, proportional breakdown of prey item sizes provisioned to the nest was significantly different between cool and hot days (Pearson's chi-squared test; cool days to nest, versus hot days to nest: $X^2_{0.05(5),\ 11.07} = 20.03$, $p < 0.05$). This difference was due to a general shift towards provisioning smaller prey items on hot days (Figure 4), suggesting fewer large prey items overall were captured on hot days.

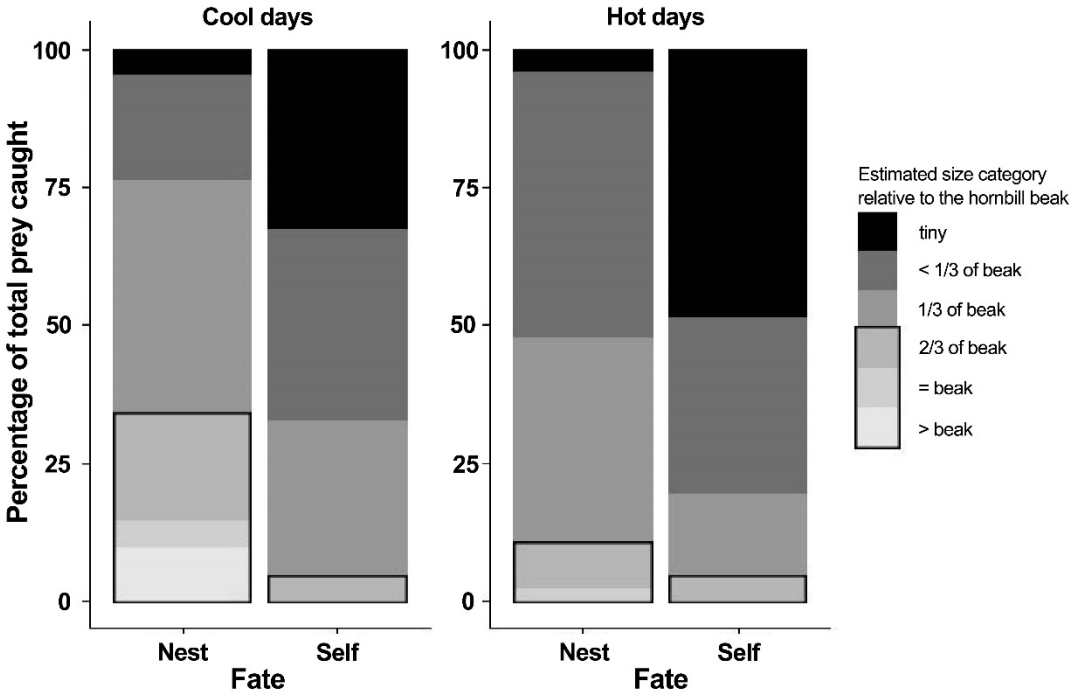

Figure 4 Comparison of the percentage of total prey items caught in each of the estimated size categories during focal observations ('tiny', '< 1/3 of the beak','1/3 of the beak', '2/3 of the beak', 'same size as the beak' and '> beak') and allocation of the prey item 'nest' or 'self' on cool days (T_{max} < 34.5 °C) and hot days (T_{max} > 34.5 °C) by Southern Yellow-billed Hornbills. Boxed areas highlight "large" prey (ie larger than 1/3 of the beak). Data were derived from 104 focal observations on 8 males.

3.4.3. Prey allocation to nest versus self from focal observations

The best-fit model explaining variation in the proportion of prey items that were allocated to the nest (post chick-hatch) versus consumed by the male hornbills during 30-min focal observations had a model weight of 0.453. This model contained the predictor variables T_a and male daily mean M_b. A second and third competing model (model weight 0.248 and 0.177) additionally contained the variables 'chick age' and 'brood size' (Table 2).

Table 2 Top three models explaining variation in proportion of prey allocated to the nest versus self by male Southern Yellow-billed Hornbills.

Model	df	logLik	AICc	ΔAICc	Model weight
T_a + male M_b	4	-154.45	317.2	0.00	0.453
T_a + male M_b + chick age	5	-153.98	318.4	1.20	0.248
T_a + male M_b + brood size	5	-154.32	319.1	1.88	0.177

Global model: T_a + male M_b + chick age + brood size. Random term: Individual ID nested in season
n = 149 focal observations on 11 nesting attempts of eight males.

The averaged parameter estimates of these three best-fit models indicated that the variables T_a and male daily mean M_b had a significant negative impact on the proportion of prey items

provisioned to the nest; while the effects of chick age and brood size were non-significant. Therefore, heavier males kept more prey items for themselves, as did males experiencing hotter weather conditions (Table 3).

Table 3 Factors affecting allocation of prey items to the nest (versus self) by male Southern Yellow-billed Hornbills; estimates of effect sizes, standard error, adjusted SE, z values and p values.

Variable	Estimate	Std. Error	Adjusted SE	z value	p value
T_a	-0.06	0.02	0.02	2.97	0.003
Male M_b	-0.04	0.01	0.01	4.57	< 0.001
Chick age	0.01	0.01	0.01	0.40	0.691
Brood size	-0.04	0.18	0.19	0.21	0.834

n = 149 focal observations on 11 nesting attempts of eight males.

3.4.4. Biomass allocation to nest versus self from focal observations

The best-fit model explaining the variation in the proportion of biomass provisioned to the nest versus consumed by the male hornbills had a model weight of 0.467 and contained the predictor variables T_a, chick age and brood size (Table 4). A second and third competing model contained only chick age and brood size or chick age and T_a (model weight 0.228 and 0.191, respectively).

Table 4 Top three models explaining variation in the proportion of biomass allocated to the nest versus self by male Southern Yellow-billed Hornbills.

Model	df	logLik	AICc	ΔAICc	Model weight
Chick age + T_a + brood size	6	-291.53	595.9	0.00	0.467
Chick age + brood size	5	-293.37	597.4	1.43	0.228
Chick age + T_a	5	-293.55	597.7	1.79	0.191

Global model: chick age + T_a + brood size. Random term: Individual ID nested in season
n = 104 focal observations on 11 nesting attempts of eight males.

The averaged parameter estimates of these three best-fit models indicated that the variable chick age had a significant negative impact on the proportion of biomass allocated to the nest; while the effects of T_a and brood size were non-significant (Table 5).

Table 5 Factors affecting variation in the proportion of biomass allocated to the nest versus self by male Southern Yellow-billed Hornbills; estimates of effect sizes, standard error, adjusted SE, z values and p values.

Variable	Estimate	Std. Error	Adjusted SE	z value	p value
T_a	-0.015	0.01	0.01	1.166	0.244
Chick age	-0.039	0.01	0.01	7.373	< 0.001
Brood size	-0.123	0.10	0.10	1.278	0.201

n = 104 focal observations on 11 nesting attempts of eight males.

3.4.5. Daily provisioning rate from nest cameras

Provisioning rate data were collected during a mean of 14.1 days per nest (range 3 – 25) on 25 cool days and 74 hot days in total, including 16 days when chicks were younger than 10 days, 50 days when chicks were between 11 and 30 days old and 33 days when chicks were older than 30 days. Males are single provisioners until the females leave the nest. Female departure occurred when chicks were on average 24.3 ± 6.4 days old (n = 33 nests observed during three breeding seasons). Three models for male-only provisioning rate (females and chicks in the nest) were included in the top model set (within two ΔAICc points). These included the variables T_{max} (all models), brood size and chick age (Table 6).

Table 6 Top three models explaining effects on daily provisioning rate while male Southern Yellow-billed Hornbills were single provisioners.

Model	df	logLik	AICc	ΔAICc	Model weight
T_{max} + brood size	4	-189.72	388.4	0.00	0.484
T_{max} + chick age	4	-190.67	390.3	1.88	0.189
T_{max} + chick age + brood size	5	-189.42	390.4	1.94	0.184

Global model: T_{max} + chick age + brood size. Random term: Individual ID.
n = 47 days of observations on five males.

The averaged parameter estimates of these three best-fit models indicated that the variable T_{max} had a significant negative impact on the daily provisioning rate; while the effects of chick age and brood size were non-significant (Table 7; Figure 5A).

Table 7 Factors affecting variation in the daily provisioning rate while male Southern Yellow-billed Hornbills were single provisioners; estimates of effect sizes, standard error, adjusted SE, z values and p values.

Variable	Estimate	Std. Error	Adjusted SE	z value	p value
T_{max}	-0.04	0.01	0.01	4.05	< 0.001
Chick age	0.01	0.01	0.01	0.40	0.691
Brood size	0.09	0.07	0.07	1.26	0.208

n = 47 days of observations on five males.

One single best-fit model was found for nest provisioning rates when males and females were jointly provisioning (chicks only in the nest; model included the factors T_{max} and chick age only; AICc = 420.2, df = 5, model weight 0.611). Nest provisioning rates were negatively affected by T_{max} (GLMM estimate: -0.06 ± 0.02, z = -2.95, p = 0.003) and chick age (GLMM estimate: -0.02 ± 0.01, z = -2.02, p = 0.04; Figure 5A).

Average daily provisioning rate was 50.7 ± 3.4 items day^{-1} (n = 47 days of observation at five nests) when the males were single provisioners of the nest and 32.3 ± 1.7 items day^{-1} (n = 54 days of observation at seven nests) when both male and female were provisioning.

3.4.6. Daily biomass provisioned from nest cameras

The best model fit of daily biomass provisioned to the nest by the male hornbills as single provisioners had a model weight of 0.271 and included only the predictor variable brood size. Two competing models additionally included the predictor variables T_{max} and chick age (Table 8).

Table 8 Top three models explaining effects on biomass provisioned to the nest while the male Southern Yellow-billed Hornbills are single provisioners.

Model	df	logLik	AICc	ΔAICc	Model weight
Brood size	4	-202.71	414.2	0.00	0.271
Brood size + T_{max}	5	-201.51	414.2	0.01	0.269
Brood size + T_{max} + chick age	6	-200.65	415.0	0.83	0.179

Global model: brood size + T_{max} + chick age. Random term: Individual ID.
n = 45 days of observations on five males.

The averaged parameter estimates of these three best-fit models indicated that none of the variables had a significant impact on the daily biomass provisioned to the nest (Table 9).

Table 9 Factors affecting variation in biomass provisioned to the nest while the male Southern Yellow-billed Hornbills are single provisioners; estimates of effect sizes, standard error, adjusted SE, z values and p values.

Variable	Estimate	Std. Error	Adjusted SE	z value	p value
T_{max}	-0.53	0.62	0.63	0.84	0.398
Chick age	0.11	0.25	0.25	0.46	0.649
Brood size	3.15	2.35	2.41	1.31	0.191

n = 45 days of observations on five males.

The single best-fit model explaining the daily biomass delivered to the nest when the male and female hornbills shared nest provisioning included the predictor variables T_{max} and chick age (AICc = 369.3, df = 6, model weight of 0.854). Daily biomass provisioned to the nest by male

and female combined (i.e. after the females departed and aided the males in nest provisioning) was negatively influenced by T_{max} (LMM estimate: -1.31 ± 0.41, z = -3.35, p = 0.006) and chick age (LMM estimate: -0.44 ± 0.13, z = -3.36, p = 0.006; Figure 5B).

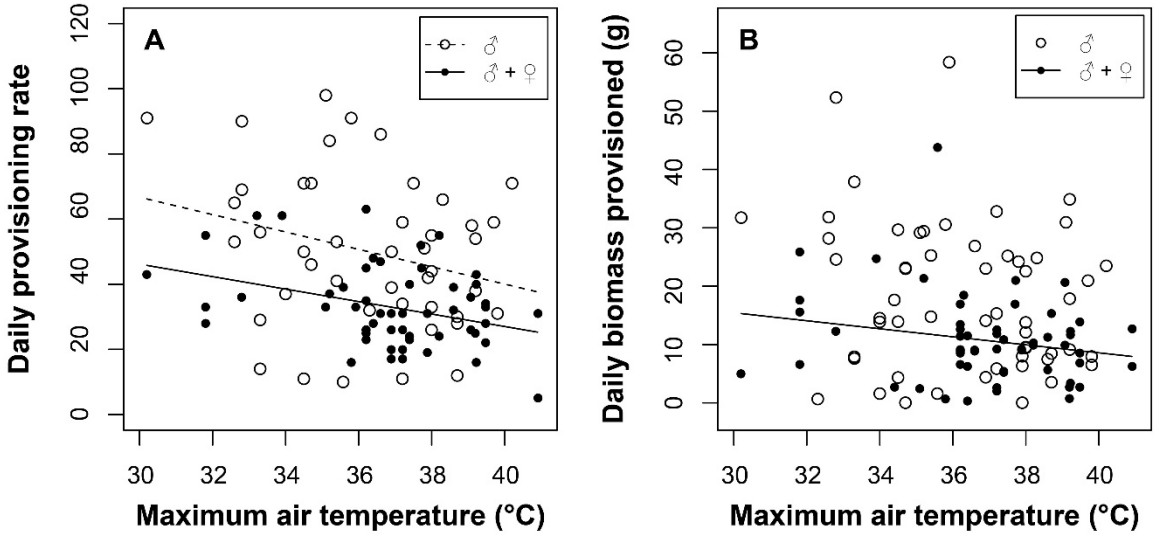

Figure 5 (A) Daily provisioning rate as a function of daily T_{max} in Southern Yellow-billed Hornbills. The dashed line represents the model predictions while the males were single provisioners and includes the variable 'T_{max}' (raw data presented as open circles). The black line represents the model predictions of the male and female shared provisioning including the variables 'T_{max}' and 'chick age' (raw data presented as solid circles). (B) Daily biomass provisioned as a function of daily T_{max}. None of the predictor variables had a significant effect on daily biomass provisioned while the males were single provisioners (raw data presented as open circles). The black line represents the model predictions of the male and female shared provisioning including the variables 'T_{max}' and 'chick age' (raw data presented as solid circles). All model predictions include individual ID nested in nest ID as a random factor. Data were derived from 99 days of camera recordings from seven nests.

3.4.7. Diurnal body mass change of males

The single best-fit model for diurnal M_b change (mass gain over 12 hours as a percentage of M_b at sunrise) in provisioning male hornbills contained only the predictor variable T_{max} (AICc = 278.3, df = 5, model weight of 0.482). Male diurnal M_b change was negatively correlated with T_{max} (LMM estimate: -0.32 ± 0.11, t = -2.85, p = 0.003) during the period from chick hatch until chick fledge. Overnight male mass loss averaged 4.5 ± 0.9 % (n = 19) and daily mean mass gain was 1.1 ± 0.4 % (n = 73). The threshold temperature above which provisioning males did not gain any mass during the course of a day was 37.9 °C, which was irrespective of chick age (Figure 6).

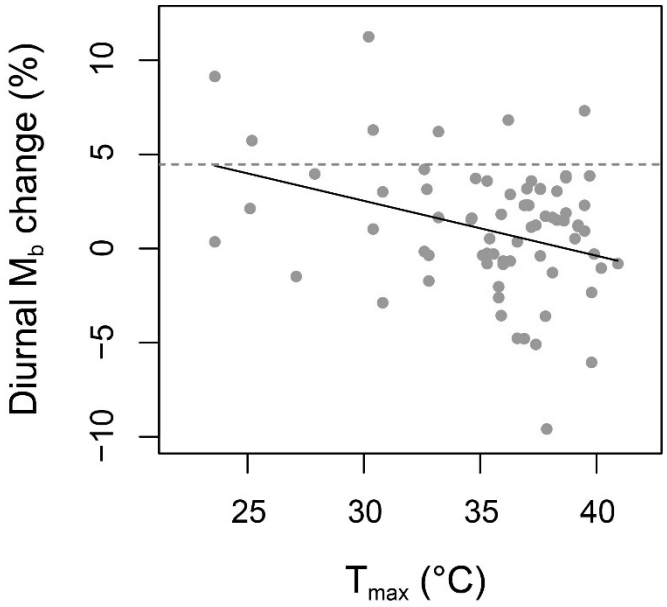

Figure 6 Diurnal M_b change (%) of male Southern Yellow-billed Hornbills as a function of daily T_{max}. The line represents the prediction from the model that includes the predictor variable T_{max} and individual ID nested within season as a random effect. Dashed line represents the overnight mass loss of 4.5 %. Data were derived from 73 days of diurnal M_b change recordings during 10 nesting attempts of 7 males.

3.4.8. Daily mean body mass of the males

The single best-fit model for male daily mean M_b during the period from chick hatch until chick fledge was explained by the predictor variables chick age, initial M_b when chicks hatched and T_{max} the day prior to M_b measurement (AICc = 810.5, df = 7, model weight of 0.897). Although mean daily M_b of the males in this study outside the breeding season is unknown, the males lost mass at an average rate of 0.69 g.day^{-1} during the nestling period (indicated by the variable chick age, which was measured in days from hatch = day 0; Figure 7). In addition, M_b was on average > 0.8 g lower for each 1°C increase in T_{max} the day prior to M_b measurement. Finally, initial M_b was positively correlated with daily M_b throughout this period (i.e. males that were heavier at chick hatch maintained higher M_b throughout the nestling period; Table 10).

Table 10 Factors affecting daily mean M_b of male Southern Yellow-billed Hornbills during the period from chick hatch to chick fledge; estimates of effect sizes, standard error, t values and p values.

Variable	Estimate	Std. Error	t value	p value
Chick age	-0.694	0.09	-7.37	< 0.001
Initial M_b	0.572	0.15	3.92	0.003
T_{max} day prior	-0.848	0.29	-2.93	0.011

n = 122 observations on 14 nesting attempts of 10 males.

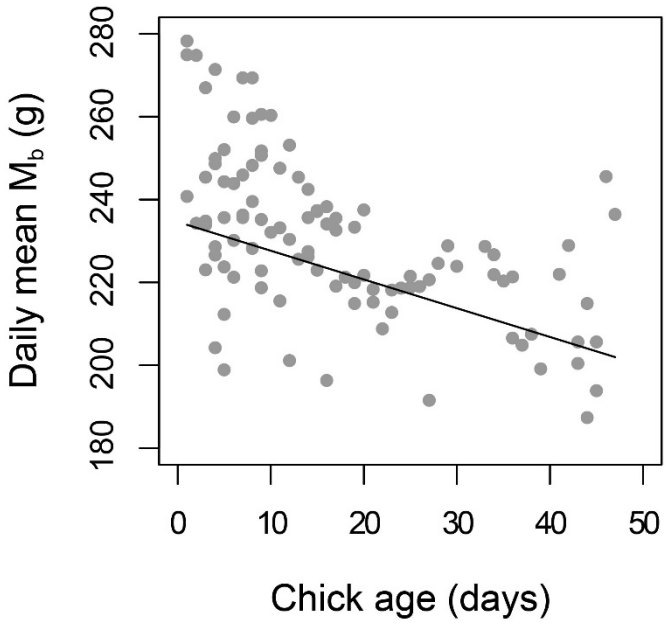

Figure 7 Daily mean male M_b (g) during the period from chick hatch to chick fledge decreased with chick age. The line represents the prediction from the model that includes the variables chick age, initial M_b and T_{max} the day prior to M_b measurement and individual ID nested within season as a random effect. Data were derived from 122 M_b measurements during 14 nesting attempts of 10 individuals across three summer seasons.

3.4.9. Nesting success

Mean T_{max} of the nestling period (between hatching of the first chick and fledging of the last chick per nest) was significantly higher for nests that failed to fledge a chick (failed nests: 36.9 ± SD 1.7 °C, n = 4; successful nests: 34.4 ± SD 1.3 °C, n = 4; t = 3.09, p = 0.01; Figure 8A) and the length of the nesting period was significantly shorter in failed nesting attempts as compared to successful nesting attempts (failed nests: 28.5 ± SD 11.4 days, n = 4; successful nests: 56.0 ± SD 8.1 days, n = 4; t = 3.94, p = 0.004; Figure 8B). There was no difference in initial male M_b at chick hatch (successful nests: 242.2 ± SD 3.0 g, n = 4; failed nests: 243.7 ± SD 4.6 g, n = 4; t = -0.25, p = 0.40; Figure 8C) or final M_b at chick fledge (successful nests: 216.3 ± SD 4.7 g, n = 4; failed nests: 218.4 ± SD 1.6 g, n = 4; t = -0.43, p = 0.33) between males of successful or failed nests.Therefore, males that failed to fledge any chicks lost significantly more mass day^{-1} during shorter and hotter nesting periods than did males of successful nesting attempts (successful nests: -0.28 ± SD 0.12 $g.day^{-1}$, n = 4; failed nests: -0.93 ± SD 0.51 $g.day^{-1}$, n = 4; t = 2.47, p = 0.02; Figure 8D).

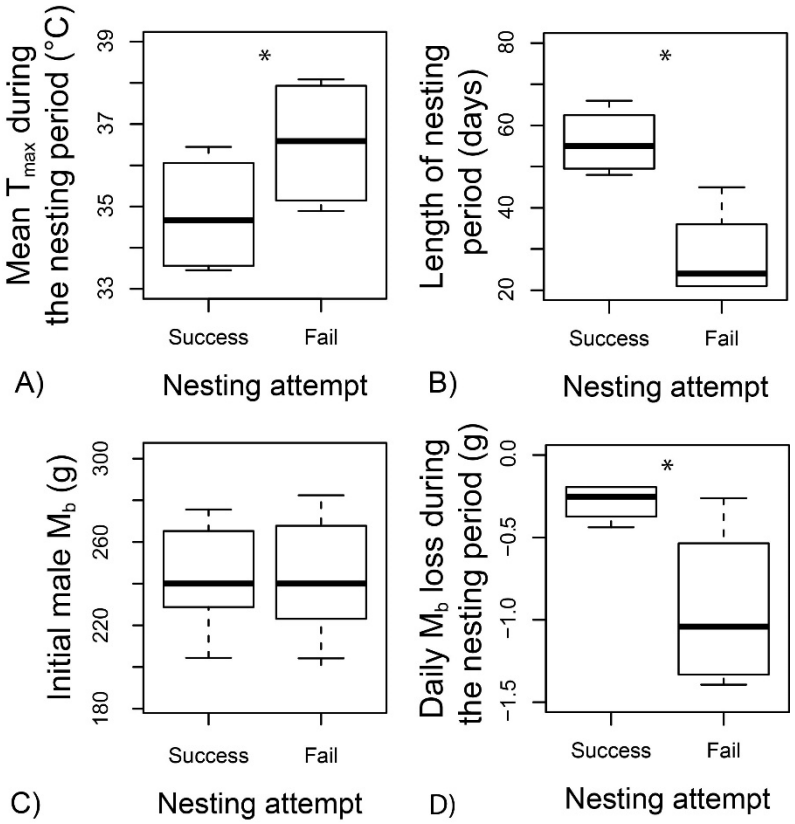

Figure 8 (A) Mean T_{max} (°C) during the nesting period, (B) length of the nesting period from chick hatch to chick fledge or fail (days), (C) initial male M_b (g) and (D) daily male M_b loss (g) during the nesting period of Southern Yellow-billed Hornbills. Data were derived from 8 males across 3 breeding seasons from which I had reliable records of M_b < 8 days after chick hatch and M_b < 9 days before chick fledge or fail. Asterisks indicate significant differences between successful and failed breeding attempts (* = α < 0.05).

3.5 Discussion

Foraging success (measured as total biomass captured per 30-min focal) by male hornbills declined when T_as increased. Larger prey items were always provisioned to the nest by the males and the small prey items caught they consumed themselves. On hot days, the males were less successful in capturing large (> 2/3 beak length) and unsuccessful in capturing very large (> beak length) prey items. Overall, heavier males minimised the number of provisioning trips to the nest to a greater extent than lighter males. Heavy males might therefore have been more experienced in making decisions about which items to provision to the nest or might have been better at capturing larger prey items. Overall, provisioning rates (but not biomass provisioned, perhaps due to errors in biomass estimation adding noise to this dataset) declined with increases in T_{max} due to reduced foraging success, and this effect remained after the females departed the nest and assisted the males in nest provisioning. During this latter period, increases in T_{max} reduced both provisioning rate and biomass provisioned. Even though males reduced energy and water requirements by reducing the number of provisioning trips on hot

days, they still lost more M_b on hot days than cool days. High T_a associated with failed nesting attempts caused males to lose M_b at a faster rate over a shorter period than successful males, but without fledging any offspring. This resulted in males of both successful and failed nests having equal M_b loss, thus paying a comparable cost for their reproductive effort, despite very different outcomes.

In this study the provisioning effort of male Southern Yellow-billed Hornbills was measured both as provisioning rate and as biomass delivered to the nest. While provisioning rate gives an estimation of the frequency of provisioning and thus includes the effort of flying to and from the nest, biomass delivered gives an estimation of how much prey mass the males are willing and able to provision to the nest. Provisioning visits to the nest decreased as it became hotter, with the males keeping for themselves a higher proportion of prey items caught. Heavier males in general allocated fewer prey items to the nest and kept a higher proportion for themselves. Due to the low sample sizes of biomass allocated and male M_b, I was unable to test whether the reduced provisioning effort of heavy males affected their decisions regarding biomass allocation. However, it seems likely that larger males made wiser decisions about which size prey items to deliver to the nest. Perhaps being able to capture larger prey items with a greater biomass, they could afford to reduce the number of travelling trips to and from the nest. One possibility that I was unable to test in this study is that heavier hornbills might be older and more experienced in capturing prey items. A study on Common Terns (*Sterna hirundo*) showed that foraging efficiency was greater in older birds due to them being more experienced foragers (Limmer and Becker, 2009). Another possibility could be that larger birds are better in defending territories with a high prey density (Adams, 2001). A second speculation on this finding is that lighter males might have a lower wing loading and therefore better flight performance (Norberg, 1981; Norberg, 1995), this could explain their increased provisioning effort perhaps at a lower flight cost (proportionally larger wing to body size than heavy birds). The prey provisioning decisions observed between lighter and heavier males could also relate to thermoregulatory demands with high T_as. Lower provisioning rates by heavier males might reflect avoidance of metabolic heat produced during flight which would be harder to dissipate passively given the lower surface area to volume ratio of larger bodies. An alternative hypothesis is that these males were heavier simply because they kept a greater proportion of prey biomass captured for themselves; thus prioritising their survival (and future reproductive success) over the current reproductive attempt. Irrespective of the actual mechanism underlying provisioning rates associated with male M_b, all males decided to make fewer provisioning trips to the nest when T_as increased resulting in lower daily provisioning rates on hot days to all nests.

In single prey loaders (like hornbills), allocation of the captured prey item is dependent on the size of the item, its nutritional value and the energetic cost of transport to the nest (Sonerud, 1989; McNamara and Houston, 1997). In keeping with this, breeding hornbill males consistently consumed the smaller prey items they caught and provisioned the larger prey items to the nest, regardless of T_a. The largest prey items (> the beak) caught by the hornbill males were always provisioned to the nest. However, the benefit to offspring of provisioning a small item (e.g. a single termite of ~ 0.02 g) would not compensate for the energy spent flying to the nest.

The proportion of prey items captured that hornbills allocated to the nest was flexible: decreasing as T_a increased, although biomass provisioned did not appear to be significantly affected by T_a (although there was a non-significant negative effect of T_a on this parameter). Flexibility in decision-making is also seen in other birds in times of unpredictable conditions during the nesting period (i.e. adverse weather or the death of a partner). For example, European Starlings (*Sturnus vulgaris*) showed flexible parental provisioning behaviour by increasing foraging effort, changing prey type and increasing prey load per provisioning trip (Wright et al., 1998). The adjusted behaviour did not affect starling M_b, but resulted in underdeveloped fledglings due to reduced nutritional value of the provisioned prey items. A study on Corsican Blue Tits (*Parus caeruleus*) showed that parent birds increased foraging distance when prey density was low, but the increased travelling and search time decreased their nest provisioning rates (Tremblay et al., 2005). These birds would instead provision larger prey items which resulted in a biomass delivery that was similar to those parents foraging in high prey density sites.

Daily provisioning rate was affected by T_{max} when males were single provisioners and when males and females were both provisioning. Besides the effects of T_{max}, decreases in provisioning rates and total biomass provisioned were also observed when chicks got older. The combined daily provisioning rate of the male and female was only 63.7 % of provisioning rate by the male alone. This finding reflects the asymptote in the growth curve of chicks that approach fledging age, when food delivered needs to meet the demands for feather growth but not body growth (Ricklefs, 1968). A lower provisioning rate of hornbill parents to their chicks could also have been intended to encourage the chicks to fledge due to reduced availability of food in the vicinity of the nest. A theory on the regulation of prey density was first proposed by Ashmole (1963) stating that foraging opportunity is lower in proximity of seabird breeding colonies. The so called “Ashmole’s halo” predicts a reduction of food provisioned to the young when food becomes depleted in areas close to the nest (Gaston et al., 2007). Likewise, the

depletion of food around hornbill nests towards the end of the nesting period might force parents and chicks to move to less depleted areas of the territory after the chicks had fledged.

The diurnal M_b change (mass gain between dawn and dusk) of the hornbill males decreased as T_{max} increased, but was not affected by chick age or brood size. However, males on average gained less mass during the day than they lost overnight, and on days hotter than 37.9°C they lost mass during the day. This inability to break even on overnight mass loss, even on cool days, is likely due to the fact that these males had to forage for themselves as well as the females and the chicks inside the nest. Diurnal changes of M_b in animals can be related to prey availability, energy gain and expenditure during activity (i.e. foraging) and / or weather conditions (du Plessis et al., 2012). In my study, foraging efficiency of male hornbills decreased when T_as increased due to behavioural thermoregulatory trade-offs (Chapter 2), as did the amount of biomass captured (this chapter). It therefore seems likely that the negative impact of hot days on diurnal M_b change of the males was driven simply by inadequate food, and therefore water, intake. A recent study identified the importance of fat reserves in arid-zone inhabitants and could provide a second explanation for how M_b was affected by increased thermoregulatory demands during hot weather. The authors showed that food and water deprived zebra finches (*Taeniopygia guttata*) catabolised fat reserves (rather than proteinaceous tissue) and thereby effectively maintained body water balance over a 24h period (Rutkowska et al., 2016), while losing body condition. Fat catabolism could be an important strategy for desert birds to maintain water balance during periods of low food and water availability, as well as during periods of high T_a when water is evaporated via panting.

Studies on diurnal M_b changes in free-ranging animals are limited due to the necessity of obtaining a dawn and dusk M_b measurement of the same individual to calculate the proportional change. Despite this, understanding factors affecting changes in diurnal M_b are very important in predicting short-term impacts on body condition. If stressors that reduce an individual's ability to maintain M_b, in this case a high daily T_{max}, occur frequently during the breeding season, M_b losses could lead to brood abandonment to secure own survival (and future reproductive opportunities). During the three breeding seasons of this study, the environmental conditions were never so extreme as to cause breeding males to sacrifice the brood. However, if the Kalahari continues to warm as predicted (Moise and Hudson, 2008), brood desertion by males might become more likely.

3.6 Conclusions

High T_a during the nesting period had adverse effects on the foraging success of breeding male hornbills. The males showed flexibility in the decisions they made in terms of prey allocation with respect to T_a, provisioning a lower proportion of the prey they captured to the nest on hot days. Despite this, males lost M_b during the course of the nesting period and their diurnal mass loss was exacerbated on hot days. Failed nests experienced significantly hotter weather conditions than successful nests, and the length of the nesting period between hatching of the first chick and fledging / death of the last chick was shorter for nests that failed to fledge any chicks. Males of unsuccessful nests lost mass at a higher rate than males of successful nests, reflecting the negative effect of high T_{max} on daily mass gain. Failed males paid the same costs of reproduction (in terms of mass loss) as successful males, but without any potential fitness payoff in the form of successfully fledged chicks. Despite this, no males abandoned their nests during the course of this study (as shown by male nest attendance up to the point of failure), suggesting that under current climate conditions the decision to abandon a reproductive attempt rests with the female parent. In the following chapter, I investigate the impacts of temperature on female reproductive investment and nestling growth and survival.

CHAPTER 4 IMPACT OF THE THERMAL ENVIRONMENT ON FEMALE BODY MASS, CHICK GROWTH AND FLEDGING SUCCESS

4.1 Abstract

Southern Yellow-billed Hornbills (*Tockus leucomelas*) breed during summer when high air temperature (T_a) could impact reproductive success, especially under ongoing climate change. Nest predation rates are low because females and nestlings are sealed inside the nest cavity. Fledging success therefore depends largely on chick growth rate which, in turn, is dependent on parental care and conditions within the nest. In this chapter I aim to understand how T_a affects female body condition and chick growth rate in the nest, and consequent impacts on fledging success and the size and mass of fledglings.

Female body mass (M_b) during the post-hatch period in the nest was strongly influenced by daily maximum air temperature (T_{max}) of the preceding day, chick age and initial M_b at nest entry. The extent of diurnal gain in M_b of the females and chicks decreased with increasing T_{max}, and in chicks was further influenced by age. Independent of chick age, the females departed the nest as their M_b approached a lower tolerance limit. The M_b and tarsus length of successfully fledged chicks was negatively influenced by mean T_{max}, and chick age at fledging was positively influenced by the effects driven by mean T_{max} during the period from hatch to fledge. The probability of a successful nest was negatively influenced by mean T_{max} during the period from hatching to fledging. Female M_b at nest entry, and chick M_b and chick age on the day the females left the nest, all positively influenced the probability of breeding success.

Of the 50 nesting attempts I recorded during the three breeding seasons included in this study, 42 % were successful. The number of hot days per year has increased in the southern Kalahari over the past two decades. My findings suggest that, if the current trend of increase in the frequency and intensity of hot days continues, hornbill reproductive success will be negatively affected. Increases in T_a in the region could place the Southern Yellow-billed Hornbill population in this part of the Kalahari at risk of local extinction.

4.2 Introduction

Understanding the impact of thermal environments on avian reproductive performance has become increasingly important with the recent increases in air temperature (T_a) globally (Visser et al., 2004; Ardia et al., 2006; Parmesan, 2006; Møller et al., 2010). Extreme low T_as affect nest success at higher latitudes (McCarty and Winkler, 1999; Dawson et al., 2005), whereas at lower latitudes nest success is more likely to be impacted by high T_as (Cunningham et al., 2013c; Salaberria et al., 2014). T_a can affect nesting success during all stages of breeding: pre-breeding condition of the parents, chick development during incubation and after chick hatch and carry over effects to post fledging survival. Body condition of parents and chicks can be affected by daily maximum air temperature (T_{max}) through increases in thermoregulatory costs and / or decreases in food availability (McCarty and Winkler, 1999; Dybala et al., 2013). Therefore, high T_a during the breeding season can reduce chick growth rates, subsequently affecting M_b of chicks at fledging and / or post fledging survival (Green and Cockburn, 2001; Braasch et al., 2008; Greño et al., 2008).

Birds may respond to hotter conditions by breeding earlier in the season (Dunn and Winkler, 1999) or by selecting cooler nest microsites (Tieleman et al., 2008). However, adjusting reproductive strategies to mitigate the impacts of the thermal environment on reproductive success may have negative consequences (Dunn and Winkler, 2010). For example, increased parental energy expenditure during incubation can limit reproductive investment of parents at later stages during chick development (Reid et al., 2000; Coe et al., 2015). Parents face trade-offs between reproductive investment and maintenance of their own body condition. Birds breeding under extremely hot conditions balance these trade-offs, but in the worst case this may lead to brood abandonment to ensure adult survival (Alrashidi et al., 2010).

Thermal trade-offs during reproduction are expected to be severe in hornbills (Bucerotidae), given the high energy demands of their breeding strategy. Hornbills are cavity breeders and the females are confined to the nest for part of the breeding season (Moreau and Moreau, 1941; Witmer, 1993; Kemp, 1995). Hornbill pairs are socially monogamous and highly territorial; males and females form a strong bond during the pre-nesting period, when the males present numerous food items to the females (Kemp, 1995; Kinnaird and O'Brien, 2007). The males' capacity to provision is crucial to the females, because soon after females settle in the nest and seal the entrance they undergo a complete moult of their flight feathers, rendering them flightless and therefore unable to forage even if they could leave the nest (Moreau, 1937; Kemp, 1995). During moult, incubation and chick rearing, the females and chicks remain entirely dependent on the males for food (Stanback et al., 2002). The energy expenditure of

female hornbills in the nest is expected to decrease due to their immobility and the consequent decrease in muscle mass (Klaassen et al., 2003). The energy requirements of the females are reduced compared to the pre-breeding period, increasing the likelihood that they can be met by the provisioning males. High T_as however will increase the females' need to keep cool via evaporative water loss, which will result in a higher demand for water-rich prey items. Female M_b might be affected on hot days if males are unable to deliver the required prey items.

In Chapter 2, I assessed the thermal trade-offs made by male Southern Yellow-billed Hornbills (*Tockus leucomelas*) and found that panting while foraging, and preference for shaded off-ground microsites, especially during hot weather, led to a decrease in foraging efficiency and overall foraging success. In Chapter 3, I found that foraging success (measured in biomass of prey captured) by males reduced with increasing T_a. Females incarcerated within the nest cavity cannot move into more thermally favourable microsites if nest temperatures become thermally stressful. Therefore, reduced food intake and increased thermal load is expected to impact M_b of breeding females through reduced water intake and increased evaporative cooling demands.

Under normal conditions, female hornbills, including the Southern Yellow-billed Hornbill, leave the nest before the chicks fledge (Kemp, 1973). The cues determining the timing of nest departure have been investigated by several authors. Mills et al. (2005) found that female Monteiro's Hornbills (*Tockus monteiri*) departed the nest at a similar M_b irrespective of chick growth, male provisioning effort and completeness of moult. Another study on the same population of Monteiro's Hornbills suggested that females departed when the energy demand of chicks peaked, alleviating the workload of the males by aiding in food provisioning (Klaassen et al., 2003). A study by Finnie (2012) on the same population of Southern Yellow-billed Hornbills addressed in my study, found that female departure was unrelated to female body condition or chick demand, but concluded instead that females depart when all the chicks in the brood are large enough to compete for food by reaching the nest entrance. If conditions in the nest become life-threatening for females and departure or abandonment of the brood is impossible due to incomplete moult, female hornbills eat their eggs or chicks in order to gain energy (Chan et al., 2007; Ng et al., 2011; Finnie, 2012).

In this chapter I assessed the impacts of T_a on female and nestling mass gain, fledgling mass and fledging success of Southern Yellow-billed Hornbills. I investigated how T_a, presumably acting via influences on biomass provisioned (Chapter 3) and internal nest conditions (this chapter), influenced female M_b, nestling growth and ultimately nest success, as measured by the number of successfully fledged chicks. I predicted that high T_a during the period that

females and chicks are in the nest would reduce nesting success through reduced diurnal M_b gain of chicks and timing of female departure. Furthermore, I expected that the period the females stayed in the nest to care for the chicks would be reduced if their own M_b was affected by high T_a.

4.3 Methods

4.3.1. Study site and population

Southern Yellow-billed Hornbills are cavity-nesters that rely on natural cavities or sites excavated by other species. At the study site, nest boxes were erected in 2008 and hornbill pairs now breed in these boxes each year. The study was conducted during three austral summer breeding seasons between October and March: 2012 / 13, 2013 / 14 and 2014 / 15. During these three seasons, 50 nesting attempts were observed of which 43 were in nest boxes and seven in natural cavities. A nesting attempt was logged when a female hornbill spent at least one day in a nest with a sealed entrance. I monitored 47 nest boxes across all three seasons and recorded breeding attempts in seven natural cavities opportunistically. Seven nest boxes had hornbills attempting to breed in them in all three seasons, six boxes and two natural cavities had breeding attempts in two seasons, 10 boxes and three cavities had one breeding attempt, and 24 monitored boxes were not used during the three breeding seasons of this study. No nest sites had more than one pair attempting to breed more than once per season and no pairs attempted to breed more than once per season. For a full description of the study site and population see Chapter 1.

4.3.2. Air and nest box temperature data collection

Weather data were collected throughout the study period from an onsite weather station (Vantage Pro2, Davis Instruments, U.S.A.) that recorded T_a (°C), relative humidity (%), wind speed ($m.s^{-1}$) and solar radiation ($W.m^{-2}$) at 5-min intervals. Thermochron iButtons (DS1923, Maxim, Sunnyvale, CA, USA, resolution = 0.0625 °C) were used to record internal nest box T_a at 5-min intervals. The temperature sensors of the iButtons were calibrated in a circulating water bath against a factory-calibrated NiCr-NiAl thermocouple (Thermocouple HH21A, Omega Engineering, Stanford, U.S.A.). Nest temperature data were collected from 14 occupied nest boxes and 2 occupied natural cavities over 219 days during three summer seasons (season 1: n = 84, season 2: n = 63 and season 3: n = 72). The iButtons were attached to the underside of the nest box lids with wall holders to minimise bird contact and to avoid interference by the female birds that often covered unfamiliar items with faeces and mud.

Deploying iButtons in occupied natural cavities was complicated by the females' tendency to remove any foreign items from the nest. In order to circumvent this, I placed the iButtons in a reader that allowed data download via a cable at some distance from the nest. The cable and iButton were secured with threading wire in the top of the tree cavity through the nest opening and hidden from the hornbill's sight by covering the wires with dough made from water, flour and salt, a method developed in the third season of data collection.

4.3.3. Nesting status data collection

Hornbill breeding activity was expected to start as early as September with the onset of rainfall, therefore from that month onwards the 47 hornbill nest boxes I monitored were checked once per week for breeding activity. All nesting locations (boxes and natural cavities) previously used by hornbills were logged by Finnie (2012) and new occupied cavities were logged by myself using a handheld GPS. The first indication of hornbills being interested in using a nesting site was the presence of a pair in the area. Both sexes inspected potential nest sites, with the females checking inside. This period of nest site exploration could take up to three months before the pairs started to apply faeces and bark around the nest opening. Eventually, the females would seal themselves inside the nest, leaving only a small opening through which food could be delivered by the males. Once the females were sealed within a nest box, they would start to moult their flight feathers.

The content of the nest boxes could be monitored by opening the box lid. Whenever an un-ringed female was encountered in a box, I collected morphometric data (wing, tail, tarsus length and M_b), a blood sample, fitted a uniquely numbered metal ring (SAFring) and a unique combination of three colour rings for field identification. Females were removed from boxes for measuring and weighing by sliding them into a pillow case, and returned to the box immediately following processing.

Nest stage was divided into four categories: "female only", "female with eggs", "female with chicks" or "chicks only". During the period "female only" and "female with eggs", female M_b was measured weekly (further details below). Approximately three weeks after egg lay, I began checking the nests daily to establish the exact hatching date of the first chick. Thereafter, I visited the nests every day to weigh the chicks and the female (see details below) and to record hatching date of subsequent nestlings. I recorded the date at which the females left the nest and the date at which each of the chicks fledged. Unfortunately, it was not possible to check the nesting status of the hornbill pairs using natural cavities, however I would record whether the pairs breeding in them successfully fledged one or more chicks.

4.3.4. Body mass data collection

I collected M_b data from all females and chicks that bred in the nest boxes. In order to minimise handling stress, females were handled within a pillow-case, so that at no stage could they see the person handling them or anything outside the nest box. The chicks were placed in small fabric bags when outside the nest. Young chicks did not show a reaction to being removed from the nest; some near-fledging chicks would occasionally vocalise when being handled, but stopped when covered by the bag. The females and all nestlings were weighed to the nearest 0.01 g on a top balance (MXX-612, Denver Instruments, Germany). Tarsus length was measured to the nearest 0.1 mm from the notch of the intertarsal joint at the back of the bird's leg to the point where the foot bends with digital calipers (SDC150, Scangrip, Denmark). After chick hatch, M_b and tarsus length were recorded twice per day, within one hour after sunrise and within one hour before sunset. This allowed estimates of diurnal M_b gain and overnight mass loss. Diurnal M_b gain was expressed as the percentage change between the morning (data collected within 1 hour after sunrise) and corrected for time between the morning and the evening (data collected within 1 hour before sunset) measurements, following the formula:

$$\Delta M_b = 100[(w2 - w1)/\, w1] \,/\, [\, \Delta t/12]$$

where ΔM_b = the diurnal M_b gain (%), w1 = morning M_b, w2 = evening M_b and Δt is the time difference (h) between the morning and evening weighing times [adapted from du Plessis et al. (2012)]. Overnight M_b loss was calculated as the average M_b loss between sunset and sunrise the following morning, standardised to 12 hour periods.

4.3.5. Statistical analyses

All analyses were conducted in the R statistical environment using R Studio interface (R Development Core Team, 2016). General linear mixed models (GLMM) and linear mixed models (LMM) were computed using the lme4 package (Bates et al., 2015) and the MuMin package was used for model selection and averaging (Bartoń, 2015). I constructed a global model that consisted of all the variables I hypothesised to have an effect on the response variable. Best-fit models were chosen based on comparison of the Akaike Information Criterion corrected for small sample size (AICc) between all possible nested models within the global models, using the "dredge" function in MuMin. Goodness of fit to model assumptions were assessed with residual plots, and results from all models with ΔAICc < 2 were presented. I used model averaged estimation of effects, standard errors and p-values when the set of best-fit models contained more than one model. Random terms were included in each model to account for non-independence due to repeated measures of individuals within seasons. Prior

to fitting global models, linear regression was used to check for collinearity of the predictor variables and correlated variables were never included in the same model. P-values < 0.05 were taken as statistically significant and mean estimates are reported ± 1 standard error (SE) unless otherwise stated.

Maximum air temperature and nesting success

Two hypothesised drivers of nesting success, daily biomass provisioned and nest temperature were predicted to be correlated with daily T_{max}. LMMs including 'nest identity' as a random factor were used to analyse these predicted relationships. These models identified strong correlations between both daily biomass provisioned and nest temperature with T_{max} (see Results). To avoid issues of multicollinearity within models, further analyses included only the variable T_{max} as a proxy for both biomass provisioned and nest temperature. Data of daily biomass provisioned were derived from 104 focal observations during 11 nesting attempts of 8 males. Nest temperature data were derived from 14 occupied nest boxes and 2 occupied natural cavities over 219 days during three summer seasons

Duration of nest stages

Duration of nest stages: The mean duration of each nest stage was calculated with respect to chick age, with hatching date taken as day 0, so that pre-laying and incubation stages had negative scores.

Comparison of successful versus failed nests: The duration of each nest stage was compared between successful and failed nests with Student's t-tests. The total time spent in the nest by females was calculated in two parts: incubation length and chick age at female departure. Lengths of these two periods, and length of the combined total (total time spent by the female in the nest) were also compared between successful and failed nests with Student's t-tests. Due to the weekly sampling interval, some (n = 6) nests already had eggs when breeding was first detected. Other nests (n = 7), I failed to note the exact dates of the duration of the breeding stages or the breeding period was too short to include in this analysis. These nests were excluded from analyses of female total time in the nest and incubation length. Data were derived from 15 successful nesting attempts in nest boxes and 22 failed nesting attempts in nest boxes.

Female body mass

Diurnal M_b change: Female diurnal M_b change (ΔM_b: calculated as the difference between dawn and dusk mass standardised to twelve hours as described above) data were available

from post-hatch to female departure from the nest, and were analysed as a LMM with a Gaussian error structure including the variables T_{max}, chick age, brood size and female M_b at nest entry with individual identity nested within season (individuals made only one nesting attempt per season) included as random terms. Data were derived from 13 females during 18 nesting attempts from which I had collected M_b at sunrise and sunset (n = 118 observations).

Daily mean M_b: I analysed female daily mean M_b (taken as the mean of M_b records of one day) separately for the period during which females were incubating, and the period during which they had chicks in the nest. These models were fitted as LMMs with a Gaussian error structure and individual identity nested within season included as a random term. In the model predicting female daily mean M_b during incubation I included the variables T_{max} of the previous day, days spent in the nest and female M_b at nest entry. Data were derived from 17 females during 27 nesting attempts (n = 103 observations). In the model predicting female daily mean M_b from chicks hatching to female departure I included the variables T_{max} of the previous day, chick age, brood size and female M_b at nest entry. Data were derived from 20 females during 30 nesting attempts (n = 323 observations).

Female M_b on nest entry and departure, comparison of successful versus failed nests: Female M_b on entering and departing the nest were compared between successful and failed nests with a Student's t-test. Data were derived from 13 females during 17 successful nesting attempts and from 11 females during 13 failed nesting attempts. I included in this analysis all females for which I had recorded M_b within 5 days after nest entry and within 5 days before nest departure.

Chick body mass

Diurnal M_b change: Diurnal M_b change (ΔM_b: calculated as the difference between dawn and dusk mass standardised to twelve hours as described above) of the chicks was analysed as a LMM with a Gaussian error structure including the variables chick age, brood size and T_{max}. Individual identity, brood identity and season were included as random terms. An additional analysis of the interaction between the predictor variables 'chick hatching order' and T_{max} did not yield a significant result and therefore no distinction was made regarding the chicks' hatching order within brood for further analyses. Data were derived from 44 chicks during 18 nesting attempts from which I had collected M_b at sunrise and sunset (n = 306 observations).

Nestling growth curves: Mean daily M_b (growth) of the chicks was assessed as a function of chick age separately for successfully fledged chicks and chicks that died, because the latter chicks had a lower growth asymptote. Non-linear models with graphical representation:

exponential, Gompertz, logistic, log-logistic and Weibull were fitted to the data and goodness of model fits were assessed by AIC value (Szabelska et al., 2010; Tjørve and Tjørve, 2010) and computed in the drc package in R (Ritz and Streibig, 2005). The growth in mass of hornbill chicks was best explained by a log-logistic relationship of chick growth *y* with chick age *x*:

$$y = f(x) = \alpha + \frac{\beta - \alpha}{(1 + exp(\gamma(lnx - ln\delta))^{\epsilon}}$$

where α is the lower limit, β is the upper limit, γ is the slope of the curve around δ. δ is the number of days where growth is 50 % of fledgling mass. If the parameter ε differs from 1 then the function is asymmetric, otherwise it is symmetric (on a log scale). The data used for this analysis were collected across three breeding seasons from 276 observations on 19 chicks that successfully fledged, and 310 observations on 56 chicks that failed to fledge.This latter group (failed-to-fledge chicks) included three chicks that did leave the nest but were depredated on the day of fledge. AIC comparison of fitted models showed that the 30 observations on these three chicks fitted the log-logistic growth of failed-to-fledge chicks, hence their inclusion in this group.

Size, mass and age of chicks at fledge: Fledgling M_b, tarsus length and age were assessed as a function of mean T_{max} during the nestling period (calculated as the mean of daily T_{max} for the period between hatching of the first chick and fledging of the last chick per nest) using LMMs with Gaussian error structure. Individual identity, brood identity and season were included as random terms within each model. Sample size was 19 successfully fledged chicks across three breeding seasons. The M_b and tarsus length data used in these analyses were the final measurements collected within 11 days before the chicks fledged (mean 3.6 days before fledge, range 0-11, note that nestling growth generally reached an asymptote ~ 11 days before fledge, Figure 7).

Factors influencing the probability of successful nesting

The probability of a successful nesting attempt was assessed using a series of GLMMs with binomial error structure, including the predictor variables mean T_{max} during the nesting period, female M_b at nest entry, chick M_b (of the first hatched chick in the brood) at female departure and chick age (of the first hatched chick in the brood) at female departure. These factors could not be fitted in one global model due to multicollinearity and were therefore analysed separately.

The dataset used for the effects of mean T_{max} and female M_b at nest entry on the probability of nest success had a sample size of 30 nesting attempts by 19 females across 3 breeding seasons. The dataset for the effects of chick age and mass at female departure had a sample size of 23 nesting attempts by 14 females across 3 breeding seasons. These differences in sample size meant AICc scores could not be compared across the four models.

Sample size was smaller than the monitored 50 nesting attempts due to limitations of the dataset of female M_b at nest entry (success: n = 17; fail: n = 13) and chick M_b and chick age at female departure (success: n = 13; fail: n = 10).

4.4 Results

4.4.1. Maximum air temperature and nesting success

Daily biomass provisioned by male hornbills was negatively correlated with T_{max} (LMM estimate: -0.88 ± 0.34, t = -2.56; p = 0.04; Figure 1A and Chapter 3), and nest temperature, as measured by iButtons within boxes and natural cavities, was positively correlated with T_{max}. The slope of the relationship between nest temperature and T_{max} was steeper for nest boxes (LMM estimate: 0.77 ± 0.01, t = 66.71, p < 0.001) than for natural cavities (LMM estimate: 0.35 ± 0.03, t = 11.92, p < 0.001; Figure 1B).

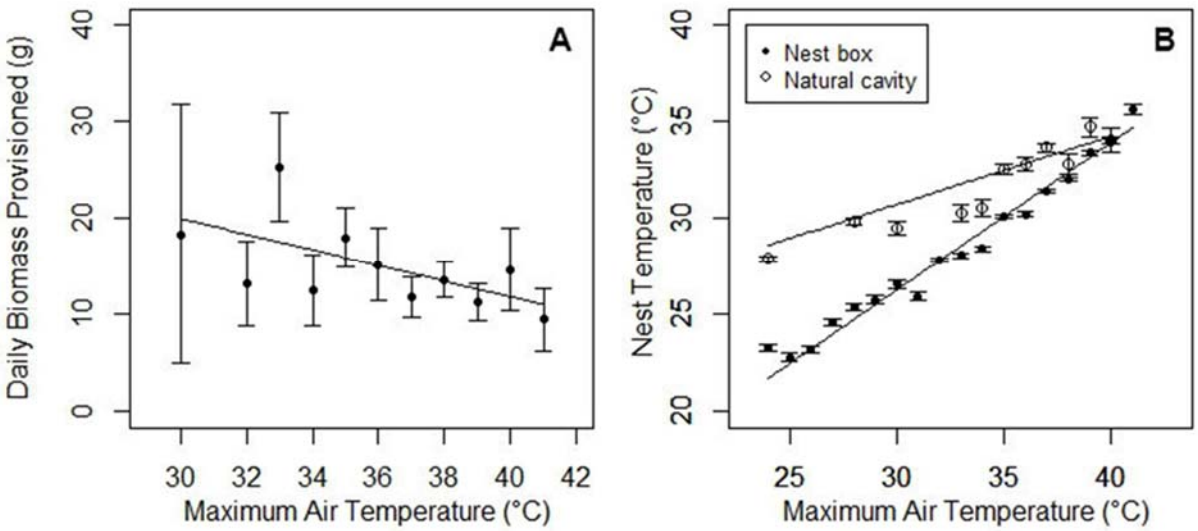

Figure 1 (A) Daily biomass provisioned by male Southern Yellow-billed Hornbills to their nests as a function of T_{max} and (B) nest temperature as a function of T_{max}. Provisioning data were drawn from 104 focal observations on 8 males. Nest temperature data were collected from 14 occupied nest boxes (black circles) and 2 occupied natural cavities (white circles) over 219 days during three summer seasons. Symbols represent mean values, lines represent the best-fit of the LMM and error bars represent 1 SE.

4.4.2. Duration of nest stages

The average incubation period was 23.8 ± SD 3.5 days (18 – 27, n = 37) and was not significantly different between successful (n = 15) and failed (n = 22) breeding attempts (t = 0.95, p = 0.18). Of the 15 nests that successfully fledged chicks, the females stayed with the chicks in the nest for an average period of 26.6 ± SD 4.0 (23 – 37) days post-hatch, and left the nest 58.4 ± SD 7.8 (49 – 76) days after they entered the nest. Of the 22 nests that failed to fledge any chicks the females stayed with the chicks in the nest for 16.6 ± SD 8.5 days post-hatch (3 – 32; success vs fail; t = 3.76, p < 0.001) and left the nest 44.8 ± SD 13.1 days (26 – 75; success vs fail; t = 3.51, p < 0.001) after they entered the nest, both significantly shorter than females with successful nests. The 11 nests that failed had chicks surviving for 14.7 ± SD 10.4 days (3 – 23) after the females departed. Chicks that fledged remained in the nest on their own for an average of 19.7 ± SD 7.4 (9 – 32; success vs fail; t = 6.65, p < 0.001) days while being fed by both parents. Successful chicks fledged the nest 78.3 ± SD 6.8 (69 – 90) days after the females first entered the nest and the first-hatched chicks per brood had an average age of 46.0 ± SD 6.5 days (35 – 57) when fledging (Figure 2).

Twenty-two failed nesting attempts of hornbills were recorded during three breeding seasons. In most of these, the females left eggs or chicks behind in the nest and chicks that were still alive did not survive more than 9 days without the females' care. The earliest abandonment date post entry was after only one day spent in the box/cavity (n = 2, not included in the analysis). Nests in which eggs were laid, but which subsequently failed to fledge any chicks did so for several reasons: the eggs were infertile or embryos died during incubation (n = 1), the females left the nest early and abandoned the eggs (n = 3), the females ate the eggs (n = 2) or chicks (n = 5), or the females left the nest early while the chicks were still dependent on their care in the nest and they eventually died (n = 8) or were depredated (n = 3).

Figure 2 The interquartile range and median of the duration of nest stages as a function of hatching date of the first chick: pre-lay, incubation, female with chicks, female departure, chicks in the nest only, chicks died and chick fledge. Data were collected across three breeding seasons from 15 nests that successfully fledged one or more chicks and 22 nests that failed to fledge chicks. Asterisks indicate significant differences between the nest stages of successful and failed breeding attempts (* = α < 0.001).

Some observations in the field are worth noting: in one nest the female died during incubation of three eggs. Fresh invertebrates in the nest confirmed that the male had been attempting to feed her. In three failed nests the chicks were unable to re-seal the nest opening and were depredated on day 3, 9 and 23 after the females had left. In one nest the female ate her two chicks that were then two and four days of age and remained in the nest together with the remaining two eggs for another 17 days, presumably to complete her moult, after which she came out leaving the eggs unhatched.

4.4.3. Diurnal female mass change

Diurnal female mass change was explained by a single best model that included the predictor variables T_{max} and brood size (AICc = -298.9, df = 6, model weight of 0.647). No other candidate models were within two ΔAICc points of this top model. Chick age and M_b at nest entry were additionally included in the global model but did not appear in the top model, and were therefore not important predictors of diurnal M_b change in females.

Each degree Celsius increase in daily T_{max} led to a 0.3 % decrease in diurnal female M_b gain (LMM estimate: -0.27 ± 0.09, t value: -3.08). Diurnal M_b gain was positively correlated with

broodsize (LMM estimate: 1.08 ± 0.39, t = 2.79). Overnight female mass loss averaged 3.5 ± 0.3 % (n = 101) and diurnal mean mass gain was 0.7 ± 0.3 % (n = 118). Females therefore lost M_b throughout the period they spent in the nest, but this loss was exacerbated by high T_{max}. The threshold T_{max} above which nest-bound females gained zero mass during the course of a day was ~ 31.4 °C (Figure 3).

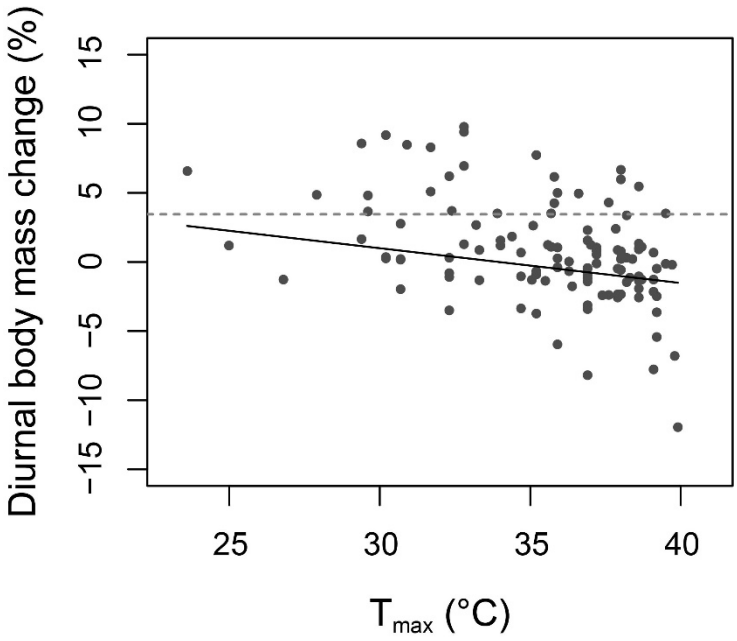

Figure 3 Diurnal M_b change (expressed as % of morning mass) of female Southern Yellow-billed Hornbills as a function of daily T_{max}. The line represents the prediction from a GLMM that included the predictor variables T_{max} and brood size; individual ID nested within season was used as a random effect. Dashed line represents the average overnight mass loss of 3.5 %. Data were derived from 118 observations on 18 nesting attempts of 13 females.

4.4.4. Female daily mean mass change

During the incubation period: M_b data collected during the incubation period consisted of 103 samples from 17 females during 27 nesting attempts. The best-fit model explaining variation in female M_b during the incubation period had a model weight of 0.430 and included only M_b at entry as the predictor variable. A competing model within two ΔAICc points also included the variable T_{max} of the day before (Table 1).

Table 1 Top two models explaining daily mean M_b of female Southern Yellow-billed Hornbills during incubation.

Model	df	logLik	AICc	ΔAICc	Model weight
M_b entry	5	-444.43	899.5	0.00	0.430
M_b entry + T_{max} day before	6	-443.40	899.7	0.19	0.392

Global model: T_{max} day before + days spent in the nest + M_b entry. Random term: Individual ID nested in season. n = 103 observations on 27 nesting attempts of 17 females.

The averaged parameter estimates of these two best-fit models indicated that female M_b at nest entry had a significant positive impact on female M_b during incubation; while the effect of T_{max} the day before was negative but non-significant (Table 2).

Table 2 Factors affecting daily mean M_b of female Southern Yellow-billed Hornbills during incubation; estimates of effect sizes, standard error, adjusted standard error, z values and p values.

Variable	Estimate	Std. Error	Adjusted SE	z value	p value
M_b entry	0.818	0.10	0.10	8.16	< 0.001
T_{max} day before	-0.326	0.55	0.55	0.59	0.555

n = 103 observations on 27 nesting attempts of 17 females.

During the nestling period: During the period that females were caring for their chicks inside the nest (post-hatch to female departure) a total of 323 records of M_b were collected from 20 females across 30 nesting attempts in three seasons. For the period after the chicks hatched, the best-fit model explaining the variation in female M_b included the predictor variables T_{max} of the preceding day, chick age, brood size and M_b at nest entry and had a model weight of 0.485. A second competing model (model weight 0.433) excluded the variable 'brood size' (Table 3).

Table 3 Top two models explaining daily mean M_b of female Southern Yellow-billed Hornbills post-hatch to female departure.

Model	df	logLik	AICc	ΔAICc	Model weight
T_{max} day before + chick age + brood size + M_b entry	8	-1296.32	2609.1	0.00	0.485
T_{max} day before + chick age + M_b entry	7	-1297.48	2609.3	0.23	0.433

Global model: T_{max} day before + chick age + brood size + M_b entry. Random term: Bird ID nested in season.
n = 323 observations on 30 nesting attempts of 20 females.

The averaged parameter estimates of these two best-fit models indicated that the variables T_{max} of the preceding day and chick age had a significant negative impact on daily mean M_b and M_b at nest entry had a significant positive impact on daily mean M_b of the females after the chicks had hatched, while the effects of brood size were non-significant (Table 4, Figure 4).

Table 4 Factors affecting the daily mean M_b of female Southern Yellow-billed Hornbills from hatching to female departure; estimates of effect sizes, standard error, z values and p values.

Variable	Estimate	Std. Error	Adjusted SE	z value	p value
T_{max} day before	-0.774	0.24	0.24	3.23	0.001
Chick age	-2.096	0.15	0.15	14.25	< 0.001
Brood size	-0.178	0.91	0.92	0.19	0.846
M_b entry	0.390	0.11	0.11	3.45	< 0.001

n = 323 observations on 30 nesting attempts of 20 females.

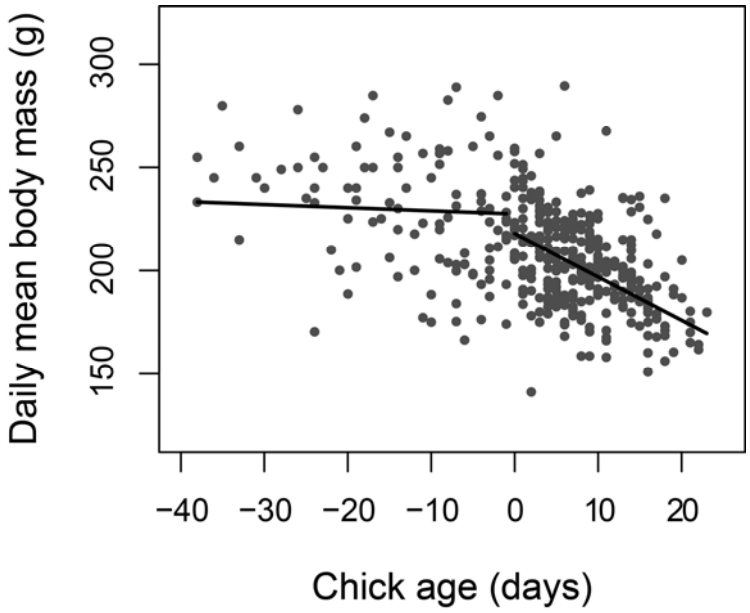

Figure 4 Daily mean M_b of female Southern Yellow-billed Hornbills as a function of chick age (zero being the hatching date); individual ID nested within season was used as a random effect. The lines represent predictions of the best-fit models for the pre-hatch and post-hatch period (n = 426 observations of 40 nesting attempts of 23 females).

4.4.5. Female body mass at nest entry and nest exit

Females that successfully fledged chicks were significantly heavier (251.2 ± SD 18.1 g) when they entered the nests than unsuccessful females (209.2 ± SD 19.4 g; success vs fail; $t = 5.23$, $p < 0.001$), however, there was no significant difference in mass at nest exit of successful (191.6 ± SD 26.1 g) and unsuccessful females (178.6 ± SD 19.3 g; success vs fail; $t = 1.30$, $p = 0.10$, Figure 5). Mean M_b when females departed the nest was 189.3 ± SD 18.1 g (150 – 246 g) for both successful and unsuccessful females.

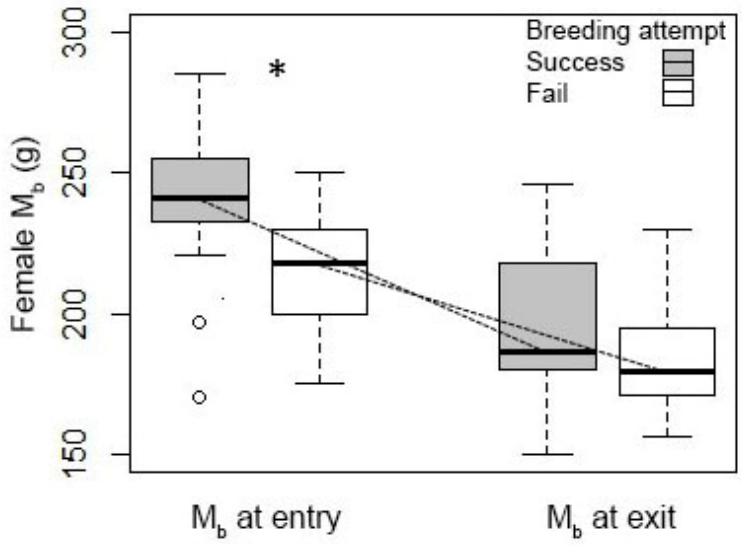

Figure 5 The interquartile range and median of daily mean M_b of female Southern Yellow-billed Hornbills on the day of nest entry and the day of nest exit between successful (n = 17 attempts by 13 females across 3 seasons) and failed breeding attempts (n = 13 attempts by 11 females across 3 seasons). Asterisk indicates significant difference (p < 0.001).

4.4.6. Diurnal body mass change of the chicks

The diurnal M_b change as a percentage of the morning M_b in chicks was collected over three breeding seasons from 44 chicks during 16 nesting attempts. The best-fit model for diurnal M_b change contained the predictor variables T_{max} (of that day), chick age and brood size and had a model weight of 0.596. A competing model within two ΔAICc contained only the variables T_{max} and chick age (Table 5).

Table 5 Top two models explaining diurnal M_b change of Southern Yellow-billed Hornbill chicks during the period from hatching to fledging.

Model	df	logLik	AICc	ΔAICc	Model weight
T_{max} + chick age + brood size	7	-1123.77	2261.9	0.00	0.596
T_{max} + chick age	6	-1125.53	2263.3	1.42	0.293

Global model: T_{max} + chick age + brood size. Random terms: individual ID, brood ID and season.
n = 306 observations on 44 chicks.

The averaged parameter estimates of these two best-fit models indicated that the predictor variables T_{max} and chick age had a significant negative impact on chick diurnal M_b change, however, brood size did not predict chick diurnal M_b change significantly (Table 6; Figure 6).

Table 6 Factors affecting diurnal M_b change of Southern Yellow-billed Hornbill chicks during the period from chick hatch to chick fledge; estimates of effect sizes, standard error, z values and p values.

Variable	Estimate	Std. Error	Adjusted SE	z value	p value
T_{max}	-0.927	0.17	0.17	5.55	< 0.001
Chick age	-0.489	0.05	0.05	9.05	< 0.001
Brood size	-0.865	0.98	0.99	0.88	0.380

n = 306 observations on 44 chicks.

Overnight mass loss of chicks was on average 7.1 ± 0.5 % (n = 227) and chicks were unable to make up for overnight mass loss when T_{max} exceeded 40.58 °C. This threshold value is much higher than the threshold T_{max} above which nest-bound females gained zero mass (~ 31.4 °C), because besides maintenance, chicks need to gain weight daily in order to grow.

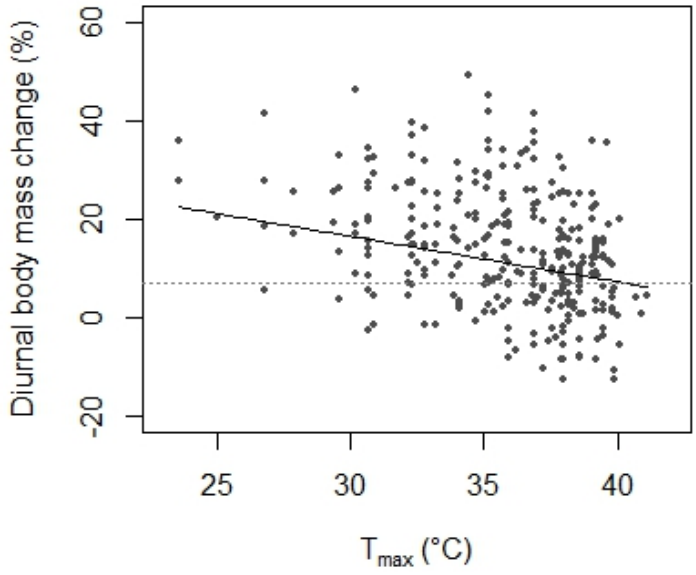

Figure 6 Diurnal mass change (%) of Southern Yellow-billed Hornbill chicks as a function of T_{max}. The line represents the prediction from the model that includes the predictor variables T_{max} and chick age. Individual identity, brood identity and season were included as random terms. Dashed line represents the overnight mass loss of 7.1 %. Data were derived from 306 observations on 44 chicks.

4.4.7. Chick growth rates

Hornbill chick growth rates (grams per day; $g.d^{-1}$) were best described by a log-logistic model. Chicks that fledged successfully gained 4.98 ± 0.16 $g.d^{-1}$, reached 50 % growth after 36.5 ± 1.1 days and reached a growth asymptote of 210.2 ± 4.3 g. Chicks that died in the nest or were depredated on the day of fledging gained on average 2.79 ± 0.17 $g.d^{-1}$, reached 50 % of final mass after 39.6 ± 1.8 days and reached a growth asymptote at 146.9 ± 4.4 g (Table 7; Figure 7).

Table 7 Parameters describing growth rates of Southern Yellow-billed Hornbill chicks that fledged successfully (n = 19) and those that failed to fledge (n = 56); estimates of effect sizes, standard error, t values and p values.

Nesting outcome	Parameters	Estimate	Std. Error	t value	p value
Successful fledge	γ: slope	4.98	0.16	31.80	< 0.001
	α: lower limit	6.85	4.63	1.48	0.140
	β: upper limit	210.18	4.34	48.43	< 0.001
	δ: 50 % growth	36.47	1.09	33.56	< 0.001
	ε: assymetry	0.05	0.02	2.49	0.014
Failed fledge	γ: slope	2.79	0.17	16.82	< 0.001
	α: lower limit	6.36	2.49	2.55	0.011
	β: upper limit	146.86	4.44	33.10	< 0.001
	δ: 50 % growth	39.62	1.76	22.57	< 0.001
	ε: assymetry	0.04	0.02	2.36	0.019

n = 276 observations on 19 successfully fledged chicks and n = 310 observations on 56 failed to fledge chicks

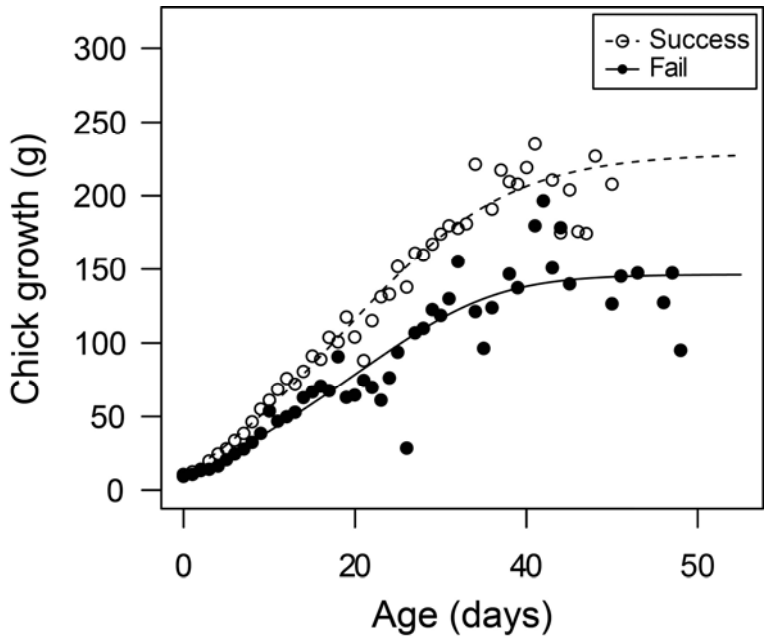

Figure 7 Daily mean M_b (g) as a function of chick age (days) of Southern Yellow-billed Hornbill chicks for successfully fledged chicks ('success': white circles, n = 276 of 19 chicks) and for chicks that died before fledging or on the day of fledge ('fail': black circles, n = 310 of 56 chicks). Data points represent the least squares estimation of the five-parameter log-logistic model. Lines represent the best-fit log-logistic model ('success': dashed line and 'fail': solid line).

4.4.8. Chick structural development at fledging

For those chicks that fledged successfully (n = 19), with every 1 °C increase in mean T_{max} during the period that the chicks were in the nest, pre-fledging M_b (measured within 11 days prior to fledging) was 20 g lower (LMM estimate: -19.95 ± 3.41, t = -5.86, p < 0.001; Figure

8A); tarsus length at fledging was 0.9 mm shorter (LMM estimate: -0.87 ± 0.27, t = -3.18, p = 0.006; Figure 8B); and age at fledge increased by 2.6 days (LMM estimate: 2.61 ± 0.74, t = 3.53, p = 0.003; Figure 8C).

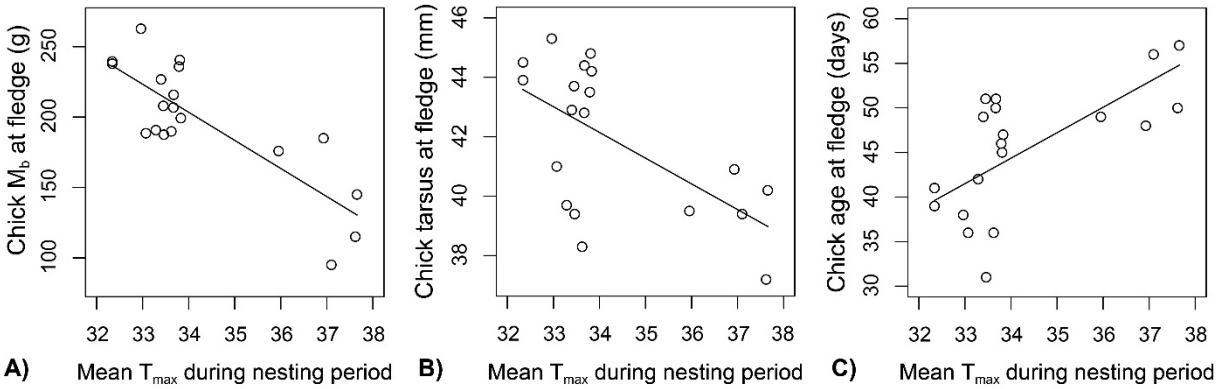

Figure 8 Southern Yellow-billed Hornbill M_b (A), tarsus length (B) and age (C) at fledging as a function of mean T_{max} during the nestling period based on 19 successfully fledged chicks across three breeding seasons. The line represents the prediction from the model with the fixed factor mean T_{max} during the nesting period. Individual identity, brood identity and season were included as random terms.

4.4.9. Probability of breeding success

The probability of chicks successfully fledging was negatively affected by mean T_{max} during the nestling period (Est. -1.40 ± 0.64, p = 0.02), falling below 50 % when mean T_{max} exceeded 35 °C (Figure 9A). The probability of nest success was also related to female M_b on nest entry (Est. 0.08 ± 0.03, p = 0.01), falling below 50 % if female initial mass was < 220 g at nest entry (Figure 9B). For chicks that survived until female departure, the probability of fledging was related to their mass (Est. 0.03 ± 0.01, p = 0.01) and age (Est. 0.15 ± 0.05, p = 0.01) when the females left the nest. If chick mass was > 122 g when the females departed (Figure 9C) or chick age > 29.8 days (Figure 9D), then the probability of fledging was > 50 % (i.e. the chicks were more likely to fledge than not).

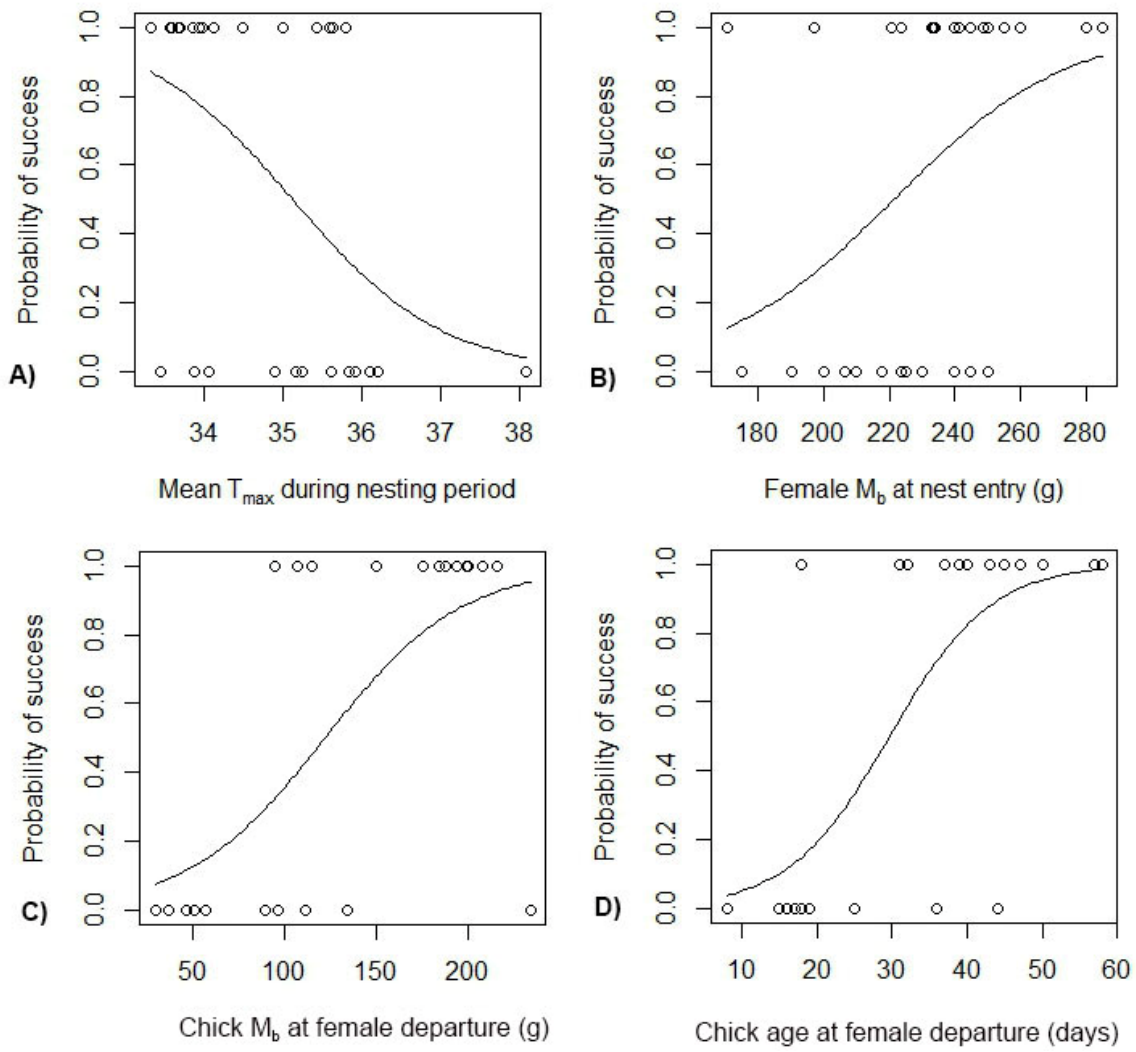

Figure 9 Probability of nesting success in Southern Yellow-billed Hornbills as a function of mean T_{max} during the chick nesting period (A), female M_b at nest entry (B), chick M_b (C) and age (D) when the females departed the nest. The line represents the prediction from the model with a binomial distribution, chick ID nested within season was used as a random effect. Data were derived from 13 successfully fledged chicks and 10 chicks that failed to fledge.

Mean T_{max} and female M_b at nest entry indirectly as well as directly affecting nesting success, by affecting the age and mass of nestlings when females departed the nest. Mean T_{max} during the nestling period was negatively correlated with the M_b chicks were able to obtain by the time females departed the nest (Est. -31.6 ± 9.20, p = 0.003; Figure 10); whereas female M_b at nest entry was positively correlated with both chick M_b (Est. 1.15 ± 0.45, p = 0.02) and chick age (Est. 0.30 ± 0.10, p = 0.006) on the day that they leave the nest. Relationships between mean T_{max} during the nestling period, female M_b at nest entry, chick M_b and chick age at the time the females leave the nest, and probability of nest success are summarised in Figure 10.

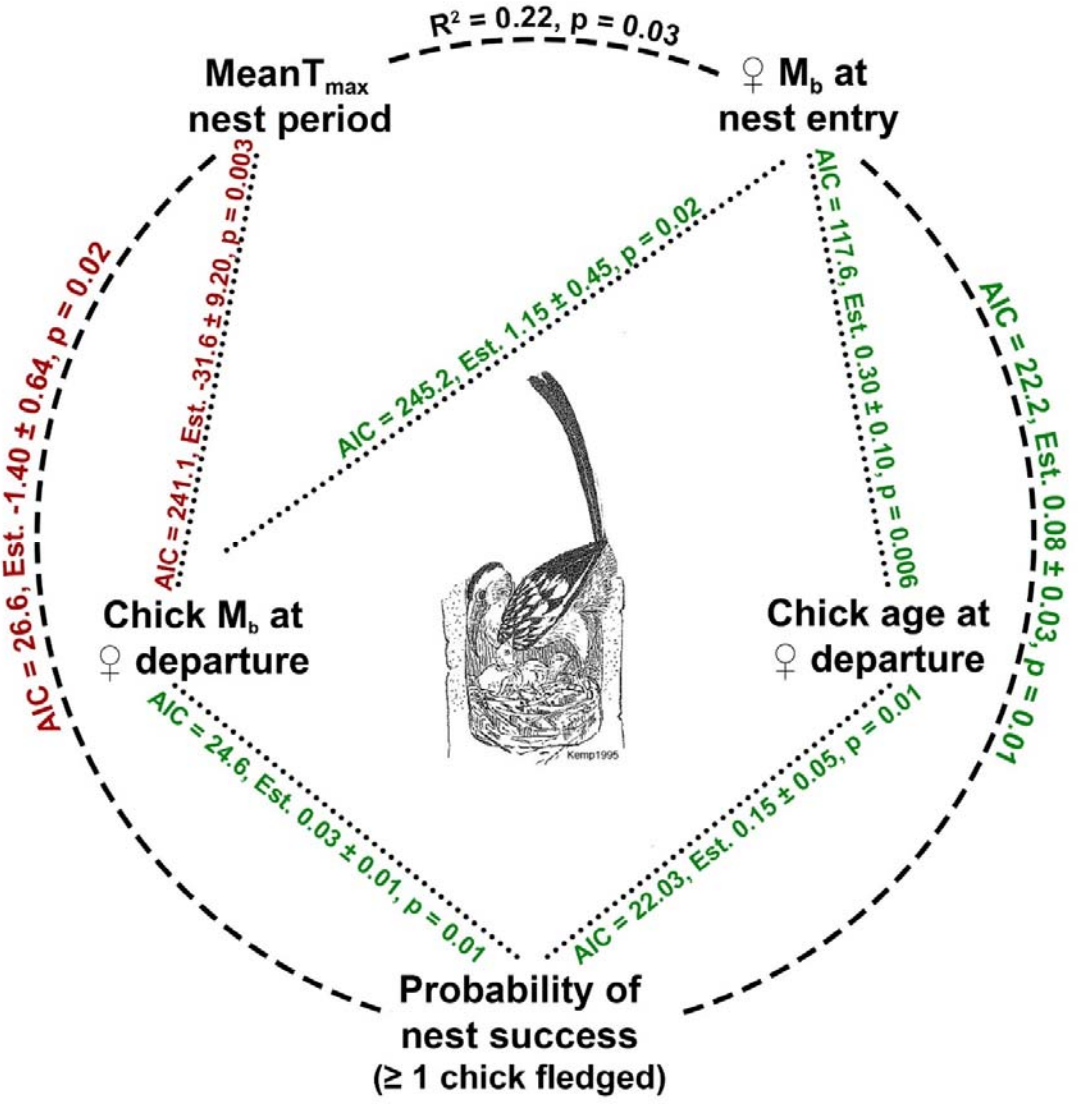

Figure 10 Probability of nest success of Southern Yellow-billed Hornbills was positively affected by female M_b at nest entry, and was negatively affected by high T_a during the nesting period. Mean T_{max} of the nesting period and female mass at nest entry were correlated, therefore separate models were fitted for their effects. Positive relationships are shown in green and negative relationships in red. Chick mass and age at female departure were both significant predictors of nest success, with older, heavier chicks more likely to fledge. Data presented on the dashed lines were derived from 17 successful and 13 failed nesting attempts. Data presented on the dotted lines were derived from 13 successful and 10 failed nesting attempts.

4.5 Discussion

High T_a during the nesting period had a negative effect on the outcomes of hornbill breeding attempts at multiple levels, and the overall effect of mean T_{max} > 35 °C during the nesting period resulted in less than 50 % probability of any chicks fledging from the nest. Nesting success was positively correlated with chick growth which in turn seemed to be associated with T_a, likely acting via its influence on temperature inside the nest and parental care (measured as biomass provisioned to the nest by the males and length of time that the females remained in

the nest). Chick growth slowed down as chicks got older, however daily mass gain was reduced on hot days for chicks of all ages. Therefore, chicks experiencing fewer hot days in the nest grew at a higher rate and had a higher probability of fledging from the nest. Females that entered the nest with M_b > 220 g could afford to lose more mass during their time in the nest and were thus able to care for the chicks in the nest for a longer period, which had a positive effect on the probability of any chicks fledging. During incubation, female M_b was only affected by their M_b at nest entry and not by high T_{max} of the previous day or by the number of days spent in the nest, suggesting that during incubation, males are able to provide sufficient prey items (energy and water) to females for M_b maintenance and thermoregulation during hot weather. This changed after the chicks hatched: female M_b was then negatively affected both by hot weather on the day prior to M_b measurement, and with every additional day that they spent in the nest with the chicks. This suggests that males were not able to provide adequate resources to the nest for female M_b maintenance and chick growth, especially during hot weather when demands are likely increased (due to the water and energy costs of evaporative cooling) (Tieleman et al., 2004; McKechnie and Wolf, 2010). The period that the females stayed in the nest with the chicks and the number of hot days during the nesting period also affected chick size (both M_b and tarsus length) at fledging which is likely to affect chick survival after fledging (Greño et al., 2008).

High T_{max} during the nesting period had a negative association on chick development with high chick mortality in the nest, slow chick growth and chicks fledging smaller. Growth in nestling birds may be compromised by nutritional stress induced by reduced provisioning (Morrison et al., 2016), exposure to heavy metal contaminants in the environment (Spahn and Sherry, 1999) or heat stress (Yalcin et al., 1997; Cunningham et al., 2013c). Nestlings exposed to high temperatures show reduced growth rates as a result of increased thermoregulatory costs as well as a decreased provisioning of food by the parent birds (Tomback and Murphy, 1981; Murphy, 1985; Tremblay et al., 2005; Cunningham et al., 2013c). In this study, high T_as correlated with reduced parental investment and hotter nest microclimates, and these likely caused the reductions in chick growth I observed. Parental investment is associated with environmental conditions such as climate and prey abundance (Barrett et al., 1987; Henderson and Hart, 1993). In this study, parental investment was assessed through provisioning rates of the males (Chapter 3) and time that the females spent inside the nest caring for the chicks (current chapter). Both these parameters were related to the M_b of the parent birds which was in turn affected by the thermal conditions during the breeding season. Finnie (2012) observed an increased competition for food among chicks, when female hornbills were experimentally removed from the nest. The decrease in growth rate of unsuccessful chicks observed in this

study is therefore likely to be a result of females departing early. Three of the 19 hornbill chicks that fledged successfully died on the day of fledging due to being depredated. These three chicks experienced a mean T_{max} of 37.5 ± 0.3 °C during the nesting period and fledged with a lower than average M_b (118.3 ± SD 25.1 g) and undersized tarsus length (38.9 ± SD 1.6 mm). It seems possible that these chicks had not reached sufficient structural development at the time of fledge in order to be able to escape from predators. With T_as predicted to rise in the future, this would suggest that even if hornbill pairs are successful in producing a fledgling, the chicks might not be sufficiently developed to survive after fledging.

In this study, some female hornbills left the nest when their chicks had just hatched or during the last days of incubation. If conditions in the nest were suboptimal for breeding, why didn't they abandon earlier? Finnie (2012) found that flight feather moult in female Southern Yellow-billed Hornbills started after the first egg was laid and took approximately 30 days for new feathers to reach at least 80 % of maximum feather length. No females left the nest before their flight feathers reached this stage of development (Finnie, 2012). Sufficient development of the primary feathers of the wing are required for flight, so moult status likely limits timing of female departure from the nest. Indeed, females in my study which abandoned the nest, leaving eggs or dependent chicks behind, generally did so after a period of ~ 30 days after laying the first egg (30.3 ± 1.5 days, n = 13), suggesting that they left as soon as their flight feathers were grown.

Finnie (2012) concluded that successful females left the nest once the chicks had reached a certain M_b at which they could compete with their siblings and were large enough to receive food items from the nest entrance. In the current study, some females left the nest well beyond the 30 days needed for moult completion, but still the chicks failed to fledge successfully. This suggests suboptimal conditions during the three breeding seasons covered by my study forced some females to abandon the brood as they reached a lower minimum tolerable M_b, which appears to be ~ 190 g (both successful and unsuccessful females left the nest with a mean M_b of 189.3 ± SD 18.1 g). Therefore, females who had a higher M_b on the day of nest entry could afford to lose a greater proportion of initial mass than lighter females before they were forced to leave the nest. These females could stay longer in the nest, which significantly increased their probability of successfully fledging at least one chick. Prior to nest entry, females cannot predict the conditions of the coming breeding season in advance, so even light females still attempt to breed.

No hornbill males were observed abandoning a nest during the three breeding seasons included in this study (Chapter 3). In contrast, females frequently abandoned the nest, which

suggests that breeding exerts greater energetic demands on the females than on the males. Hornbill breeding strategies have a highly asymmetrical parental investment, whereby females are mostly inactive while being confined to the nest. In his study, Finnie (2012) showed that female Southern Yellow-billed Hornbills changed the length and the pitch of the begging call, in order to communicate their need for food to their partners. However, on hot days, I found that the males struggled to meet the females' demands (Chapter 3 and this chapter), resulting in a mismatch between food requirements and the rate at which food was provisioned. The positive correlation that I found between female diurnal mass change and brood size suggests that females in this study could maintain energy balance by eating the smallest chick in the nest when insufficient food was provisioned by the male. The confined females in the nest do however, have another disadvantage when compared to the male, since they cannot escape the microclimate of the nest. They are unable to lower thermoregulatory costs by seeking out cooler microsites or by performing thermoregulatory behaviours like wing-drooping as there is presumably limited air flow in the nest. Without sufficient water-rich prey items to balance thermoregulatory demands, the females could become dehydrated and be required to sacrifice the brood in order to save themselves.

The current study on Southern Yellow-billed Hornbills breeding at the Kuruman River Reserve is the first to assess the thermal properties of the nest boxes at this study site. Temperature in the artificial nest boxes matched the outside T_a closely (Est: 0.77 ± 0.01, $R^2 = 0.89$, $p < 0.001$) and differed substantially from the temperature of the natural cavities (Est: 0.35 ± 0.03, $R^2 = 0.50$, $p < 0.001$; slope of 1 being a match). This difference in thermal conditions between nest boxes and natural cavities suggests that the impact of T_a on birds breeding in nest boxes could be higher than for birds breeding in natural cavities. I observed a total of 43 hornbill pairs breeding in nest boxes across three seasons during my study. Forty percent of these breeding attempts successfully fledged one or more chicks. Due to the difficulty of finding and accessing natural nests, I observed only seven hornbill pairs breeding in natural cavities. Of these, 57 % successfully fledged at least one chick. My sample size for natural nests was too small to detect a significant difference in success between these nests and pairs breeding in nest boxes (Fisher exact test: 95 % CI = 0.06 – 3.35, odds ratio = 0.50, $p = 0.43$).

Artificial nest boxes are often provided to cavity-nesters to aid in conservation efforts (James et al., 2011; Pasuwan et al., 2011). It is however, important that the artificial nests resemble the thermal properties of the natural cavities used by the species (Ardia et al., 2006; Butler et al., 2009), which is not always the case. For example, endangered Carnaby's Cockatoos (*Calyptorhynchus latirostris*) breeding in poorly-designed artificial nest boxes in Australia

experienced nest temperatures 5 °C higher than those birds breeding in natural cavities (Wong, 2014). Due to destruction of their natural nest sites, the artificial nest boxes had a higher occupancy rate by the Carnaby's Cockatoos and could conceivably be detrimental to the breeding success of this endangered species. Carefully constructed management efforts can however also be successful in supplementing artificial nest sites to cavity-nesting birds, as evidenced by the improved reproductive success of Southern Ground-Hornbills (*Bucorvus leadbeateri*) breeding in provided timber nest-logs in South Africa (Wilson and Hockey, 2013).

I am unable to draw any conclusions regarding whether hornbills in this study breeding in natural cavities have a higher reproductive performance than those breeding in boxes, since the effects of high T_a on female M_b and chick growth were assessed from hornbills breeding in nest boxes. In addition, male partners of hornbill pairs breeding in boxes and hornbill pairs breeding in natural cavities are equally exposed to the same thermal environment outside the nest which affects their provisioning effort (Chapter 3) and likely also prey abundance (Flower et al., 2013). Reproductive success of hornbills breeding in natural cavities at the study site needs further investigation to confirm whether cavity breeding hornbills do indeed benefit from less variable nest microclimates.

4.6 Conclusions

High T_as during the nesting period negatively impact the reproductive success of Southern Yellow-billed Hornbills. The threshold value (T_a = 35 °C) predicting when the probability of nesting success drops below 50 % (i.e. more nests fail than succeed), can be helpful in predicting reproductive performance and fitness for this population of hornbills in the future as T_as increase. A higher occurrence of females abandoning broods is a likely scenario for the future, because males already appear unable to provide sufficient water-rich prey items to meet evaporative water loss requirements of females with nestlings on hot days; and the frequency of such hot days in the Kalahari is increasing as the climate becomes warmer (Figure 1; Chapter 1). If females do manage to stay in the nest long enough that their chicks can survive to fledging, then fledglings raised during hot weather might be underdeveloped and unable to survive outside the nest. Data presented in this chapter suggest that temperatures in the southern Kalahari are already near the upper limits for successful hornbill reproduction. Unless, Southern Yellow-billed Hornbills have the capacity for being phenotypically plastic in physiological mechanisms not investigated in this study, I suggest that climate warming and the associated increases in frequency, intensity and duration of hot weather events may threaten the continued persistence of this population in the future.

CHAPTER 5 REGULATION OF HEAT EXCHANGE FROM THE HORNBILL BEAK

5.1 Abstract

Beaks are increasingly recognised as important contributors to avian thermoregulation. Several studies supporting Allen's rule demonstrate how beak size is under strong selection related to latitude and / or air temperature (T_a). Moreover, active regulation of heat transfer from the beak has recently been demonstrated in a toucan (*Ramphastos toco*, Ramphastidae), with the large beak acting as a controllable heat radiator. I hypothesised that hornbills (Bucerotidae) likewise use their large beaks for non-evaporative heat dissipation, and used thermal imaging to quantify heat exchange over a range of T_as in eighteen desert-living Southern Yellow-billed Hornbills (*Tockus leucomelas*).

I found that hornbills dissipate heat via the beak at T_as between 30.7 °C and 41.4 °C. The difference between beak surface temperature and T_a abruptly increased when T_a was within ~10 °C below body temperature (T_b), indicating active regulation of heat loss. Maximum observed heat loss via the beak was 19.9 % of total non-evaporative heat loss across the body surface. Heat loss per unit surface area via the beak more than doubled at T_a > 30.7 °C compared to T_a < 30.7 °C and at its peak dissipated 25.1 $W.m^{-2}$. Maximum heat flux rate across the beak for toucans was calculated to be as high as 204.8 $W.m^{-2}$.

I speculate that non-evaporative heat dissipation may be a particularly important mechanism for animals inhabiting humid regions, such as toucans, because evaporative avenues are less efficient in humid habitats. In Southern Yellow-billed Hornbills however, this non-evaporative heat dissipation mechanism is advantageous in water scarce environments when T_a < 41.4 °C, reducing the water expenditure of evaporative cooling (panting). Alternatively, differences in beak morphology and hardness enforced by different diets may affect the capacity of birds to use the beak for non-evaporative heat loss. This is only the second taxon in which tightly-controlled regulation of radiative heat exchange via the beak has been described, despite investigations across diverse avian species (beaks normally appear to lose heat in an uncontrolled fashion), and likely reflects functional convergence across a deep phylogenetic divide.

5.2 Introduction

There is increasing evidence for the importance of beaks in avian thermoregulation (Symonds and Tattersall, 2010), with the beak identified as a significant avenue of radiative heat dissipation in a number of species (Hagan and Heath, 1980; Tattersall et al., 2009; Greenberg et al., 2012). Variation in beak size among individuals has been shown to correspond with the thermal environment during development (Burness et al., 2013) and interspecific variation in beak size is related to environmental variables (daily maximum air temperature (T_{max}), wind exposure, fresh water availability and thermal gradients) (Greenberg et al., 2012; Luther and Greenberg, 2014). Adult Toco Toucans, *Ramphastos toco*, are able to adjust blood flow to their extremely large beaks depending on thermal conditions, allowing for fine control of heat exchange from the beak. In this species, radiative heat loss via the beak averages 60 % of total radiative heat loss at air temperatures (T_as) above 28 °C (Tattersall et al., 2009). At T_as equivalent to 20-25 °C below normothermic body temperature (T_b), vasodilation of the networks below the rhamphotheca (the sheath of keratin that forms the outer surface of the beak), cause an increase in beak surface temperature (T_s). Under these conditions, the beak acts as a heat radiator, reducing the need for evaporative heat dissipation. Toucans typically inhabit humid tropical forest environments (Short and Horne, 2001), where ambient water vapour pressures reduce the potential for evaporative heat loss, likely promoting the relative contribution of radiative heat dissipation to T_b regulation. On the other hand, reduced reliance on evaporative heat dissipation probably also has an adaptive significance for water conservation in large-beaked birds inhabiting arid environments (Greenberg et al., 2012).

Hornbills (Bucerotiformes: Bucerotidae) are widespread in the Afrotropical and Indomalayan regions, with members of this taxon occupying habitats ranging from arid savannas to humid tropical forests (Kemp, 1995). Like toucans (Piciformes: Ramphastidae), hornbills have disproportionately large beaks and are a candidate for a similar mechanism of heat exchange (however see Hughes (2014). Toucans and hornbills are not close phylogenetic relatives, having diverged approximately 55 million years ago (Jarvis et al., 2014). Therefore, if the hornbill beak were to function as a finely-controlled thermal radiator, similar to toucans, this could represent an example of convergent or parallel evolution across a deep phylogenetic divide. Such a finding (or a lack thereof) would extend our knowledge of the thermoregulatory function of avian beaks and inform understanding of the drivers of beak evolution as well as providing evidence in favour of the underlying assumptions of Allen's Rule as it relates to beak morphology (Allen, 1877; Symonds and Tattersall, 2010; Danner and Greenberg, 2015). Non-evaporative mechanisms of heat loss might be expected to be particularly important in environments where water is scarce and hence water-conservation critical. Southern Yellow-

billed Hornbills (*Tockus leucomelas*) inhabiting the Kalahari Desert may be under strong selective pressure to conserve water, particularly during the summer breeding season when T_as are high. Breeding female Southern Yellow-billed Hornbills are confined within a nest cavity to care for the offspring, while males are entirely responsible for provisioning the female and chicks (Kemp, 1995). Male and female hornbills are hence both exposed to challenging thermal environments when breeding.

I investigated whether the beak of this Afrotropical hornbill is functionally similar in terms of heat flux capacities to that of the Neotropical Toco Toucan (Tattersall et al., 2009). Following similar methods to those employed by (Tattersall et al., 2009), I used thermal imaging to quantify heat fluxes in individuals experiencing a range of thermal conditions. I used birds from a wild study population in the southern Kalahari and examined heat exchange from the beak in comparison to heat exchange from other regions of the body. I predicted that surface temperature (T_s) of the beak would be regulated so as to promote heat dissipation at T_as approaching T_b, but reduce heat loss under colder conditions. I further hypothesised that due to differing parental care roles, selection may have favoured sex-specific differences in capacity to use the beak as a thermal radiator.

5.3 Methods

5.3.1. Study site and population

The individuals used in this study were captured at Leeupan Guest Farm, Northern Cape, South Africa (S 26.95652° E 021.86913°; Chapter 1, Figure 2), a neighbouring farm to the Kuruman River Reserve where the data collection for other chapters was carried out. Individuals used in this study were not part of the study population used in the previous chapters in order to avoid potential impacts of this experiment on the habituation of focal individuals. The study site is in the southern Kalahari Desert where arid savanna dominates the vegetation along a dry riverbed and dune landscape (Whitfield et al., 2015). The site is characterised by cool, dry winters and hot summers with an annual mean rainfall of 93.7 ± 38.7 mm and mean daily summer T_{max} of 34.4 ± 0.20 °C (data from the Austral summer months October to March, 2012 – 2015 at Kuruman River Reserve). In the last twenty years, T_as exceeded 34.5 °C on 93.3 ± 4.4 days per year (1995 – 2015, Van Zylsrus, ~ 25 km from the study site, South African Weather Service). Temperatures and humidity within tree cavities occupied by a female Southern Yellow-billed Hornbill with one or more chicks at the study site can range between 20.8 - 43.1 °C and 13.8 – 97.1 % RH. During incubation and early nestling-

rearing, female hornbills are confined to the nest cavity, therefore, in contrast to males, they cannot make use of cool microsites within the wider landscape.

5.3.2. Experimental protocol

In the early austral summer of October 2013, shortly prior to the breeding season, nine adult males and nine adult female hornbills were captured with spring traps (53 x 53 cm) baited with super worms (*Zophobas morio),* and transported in cotton bags to a field laboratory within 4 km of all capture sites. Morphometric measurements were taken from each individual including body mass (M_b), wing length, tarsus length, culmen length and maximum culmen height. A lateral-view photograph of the beak and body taken with a DSLR camera (Nikon D3200, Nikon Inc., Melville, U.S.A.) was used to calculate surface areas using ImageJ™, image analysis software (version 1.47, National Institute of Health, United States).

Birds were individually subjected to a ramped profile of increasing T_as inside a darkened, custom-built temperature-controlled chamber (1200 x 400 x 300 mm), constructed of corrugated plastic insulated with polystyrene (30 mm thickness). The T_a within the cabinet was regulated using a temperature-controlled water bath circulating water through 22-mm diameter copper tubing mounted on the inner wall of the cabinet (design adapted from van de Ven et al. (2013). Air mixing was achieved with a small fan allowing for a uniform T_a within the cabinet and fresh air input. Silica gel (500 g) at the bottom of the cabinet prevented increases in humidity via exhaled water vapour and was replaced before becoming saturated. A smaller chamber made of corrugated plastic with an open front and a lid on top (350 x 120 x 350 mm), was placed within the temperature-controlled chamber. Hornbills were placed individually on a perch within the smaller chamber during data collection and would generally remain in this position. Thin nylon netting (17 x 17 mm, 0.2 mm thread thickness) covered the open front of the smaller chamber to prevent the hornbill from moving outside of the field of view of the thermal imaging camera, or coming into contact with the copper piping or silica gel or otherwise injuring themselves. Prior to each experiment, each individual spent 30 min habituating to the experimental setup at the initial T_a of 15 °C. The T_a in the cabinet was increased from 15 to 45 °C and held stable at four set point T_as (15, 25, 35, 45 °C). The T_a was considered stable when it remained within 2 °C of the experimental setpoint for 10 minutes or more. The mean heating rate between each pair of setpoint T_a values was 0.7 ± 0.1 °C min^{-1}. Increasing the T_a in a ramped fashion minimised the time each bird spent in captivity. The T_a values used are within the range that birds naturally encounter in the wild at the study site.

Hornbills spent an average of 120 minutes in the chamber, during which time continuous thermographic images were collected with an infrared camera (ThermoVision A320, FLIR Systems, Danderyd, Sweden) at a frame rate of 15 frames s^{-1}. The T_a in the chamber was monitored with a NiCr-NiAl thermocouple (Thermocouple HH21A, Omega Engineering, Stamford, U.S.A.) at 5-min intervals, and T_a and relative humidity were also recorded with three Thermochron iButtons (DS1923, Maxim, Sunnyvale, CA, USA, resolution = 0.0625 °C) at 1-min intervals. The iButtons were calibrated in a circulating water bath against a factory-calibrated NiCr-NiAl thermocouple (Thermocouple HH21A, Omega Engineering, Stamford, U.S.A.). Water vapour pressures (WVP) increased with 0.0289 kPa per 1 °C T_a increment as a consequence of the bird being present in the chamber (Figure 1). However, the combination of increasing WVP and incremental increases in T_a resulted in relative humidity values being approximately constant at 26.6 ± 0.3 % during the course of measurements.

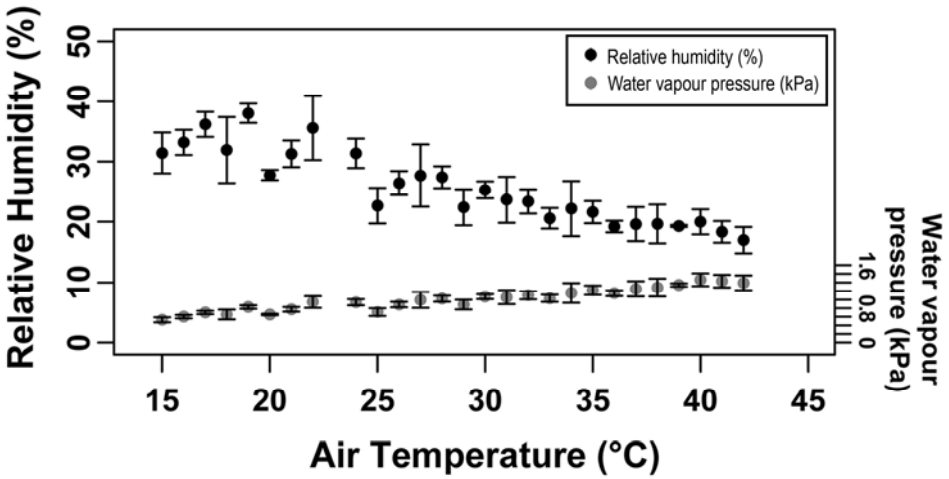

Figure 1 Relative humidity (%) (black circles) and water vapour pressure (kPa) (grey circles) in the temperature cabinet in response to T_a (°C). Data were combined from all the individual experiments. Error bars represent 1 SE.

The onset of panting in the hornbills was visually assessed from the recorded thermographic image sequence. T_b of each hornbill was measured at the start and end of each experiment to assess whether any individuals became hyperthermic during trials. A fine-gauge NiCr-NiAl thermocouple (Thermocouple HH21A, Omega Engineering, Stamford, U.S.A.) was inserted approximately 10 mm into the cloaca, a depth at which a slight withdrawal did not result in a change in the measured T_b value. Three males and one female were removed from the chamber early as they became restless at T_a < 35 °C, giving final sample sizes of 6 males and 8 females at T_a > 35 °C. T_b measurements confirmed that none of the study individuals became severely hyperthermic, with mean T_b = 41.4 ± 0.2 °C before and 42.2 ± 0.2 °C after the

experiment. All individuals were released at the site of capture immediately after completion of the experiment.

I assessed how much each region of the hornbill body contributed to overall radiative heat exchange at different T_a during the course of the experiment. For each individual, one thermal image per 2.5 °C T_a increment from 15 °C to 45 °C was sampled for T_s analysis. Preliminary analyses of these images revealed that beak T_s typically changed rapidly above a threshold T_a value. I averaged the T_a where the difference between beak temperature and T_a was greatest for the lower mandible, and total beak, for each individual in order to identify the threshold air temperature at which this change occurred (threshold T_a).

T_s analysis was done by manually selecting the area of the torso, the gular skin, the lower mandible of the beak and the entire beak in each thermal image using ThermaCAM Researcher Pro 2.9 software (FLIR Systems Inc., Wilsonville). The polygon function in this software allows for accurate selection of the body part of interest and exports the minimum, maximum and mean temperature and the standard deviation of the T_s of the selected area. The feet were excluded from this analysis since they were not always visible in the thermal images.

Morphological measurements from the individuals were modelled according to a geometric model to calculate the body part surface areas and the heat dissipated (Figure 2). The calculated feathered surface area per individual closely matched the predicted relationship of external surface area and M_b as modelled by Walsberg and King (1978). Table 1 gives an overview of the average dimensions of the different parts of the hornbill body.

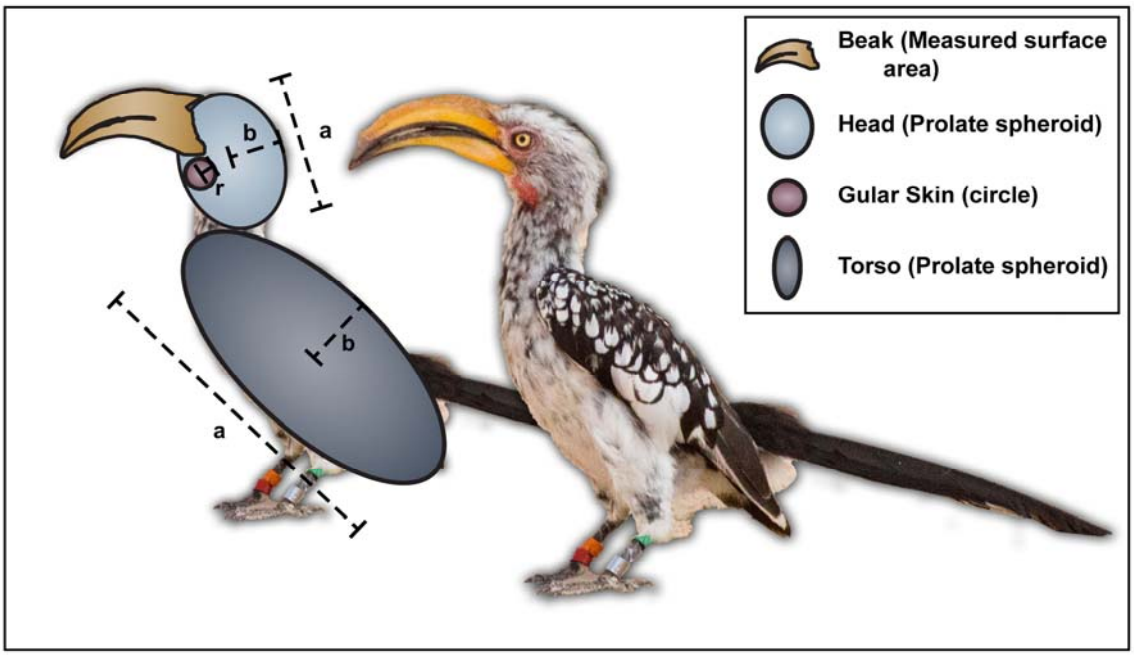

Figure 2 Measurements taken from Southern Yellow-billed Hornbills to calculate surface areas for estimates of heat transfer.

Table 1 Surface area (range), percentage of total surface area and characteristic dimensions for heat transfer calculated for the Southern Yellow-billed Hornbills.

	Surface Area (m^2)	% Total surface area	Dimension (m)	Nusselt Number
Torso	0.0620 (0.0446 - 0.0799)	94.9	0.075	Prolate spheroid 3.495
Gular Skin	0.0003 (0.0002 - 0.0003)	0.4	0.015	Flat circle 3.353
Beak	0.0031 (0.0022 - 0.0041)	4.7	0.029	Flat polygon 3.566
Total	**0.0637**			

n = 18 observations on 9 females and 9 males

5.3.3. Heat transfer calculation

In controlled conditions radiative heat transfer takes place from the bird to the environment and from the wall of the chamber to the environment (calculations following McCafferty et al. (2011) and (McCafferty et al., 2013). Radiative heat exchange can be calculated for each of the body parts of the bird with the following formula:

$$q_{rad} = A\sigma\varepsilon_a\varepsilon_w(T_s^4 - T_w^4)$$

Where A (m^{-2}) represents the surface area of each body part, σ is the Stefan-Boltzmann constant (5.67 x10^{-8} W.$m^{-2}K^{-1}$), ε_a is the emissivity of bird plumage (0.95) and ε_w is the emissivity of the white plastic walls of the bird chamber (0.84). T_s and T_w are the radiative surface temperature of the surface of the body part and the surface of the wall (°K). A small

fan in the chamber provided the bird with fresh air and prevented a decrease in oxygen levels and an anemometer recorded air flow in the chamber during the experiment. The movement of air caused by the fan did not create a measurable air flow and therefore convective heat transfer occurred via free convection and was calculated as:

$$q_{conv} = Ah_c\left(T_s - T_a\right)$$

Whereby *A* (m^2) represents the surface area of each body part, T_s is the surface temperature of the body part (°K) and T_a is the air temperature (°K). h_c is the convective heat transfer coefficient and can be calculated as follows:

$$h_c = Nu\frac{k}{d}$$

k represents the thermal conductivity of air, determined at each T_a ($W.m^{-2}$ $°K^{-1}$), d (m) is the characteristic dimension of each body part and Nu is the dimensionless Nusselt number. The Nusselt number is a measure of the ratio of buoyant to viscous forces and is dependent on the shape of the characteristic body part (Monteith and Unsworth, 2013). In order to measure the conductive heat loss, the temperature difference between the bird and any object it touches needs to be taken into account. During this experiment the bird body only came into contact with the perch via the feet. I ignored conductive heat loss, because of the low conductivity of wood (0.12 $W.m^{-2}K^{-1}$) and small surface contact of the feet on the perch. I did not attempt to measure evaporative heat loss in this study, but instead I recorded the chamber temperature at which the bird initiated panting behaviour. The total heat loss from the hornbill body was therefore only calculated below the panting initiation temperature as the sum of the radiative and conductive heat transfer:

$$q_{tot} = q_{conv} + q_{rad}$$

The contributions of the different body regions to total heat dissipation were expressed as mean heat dissipation (Watts, W), mean percentage of the total body heat dissipation, and relative heat dissipation ($W.m^{-2}$) below and above the beak threshold T_a. This was done in order to be able to assess the fractional contribution of each body region to total heat exchange, taking into account convective and radiative heat exchange (but not evaporative and conductive heat exchange). These estimates were then used to calculate heat flux per body region as a percentage of the total. T_as above hornbill T_b (41.4 ± 0.2 °C, data collected from study individuals) were not included in this analysis, because the T_{s_beak} at this stage was cooler than T_a, resulting in a negative flux value. At these high T_a values, the hornbills were

observed to pant, indicative of a switch to evaporative water loss as the primary mode of heat dissipation.

5.3.4. Data analysis

Differences in panting and beak threshold T_a in response to chamber temperature between males and females was assessed with a Welch two sample t-test (Zar, 1999). Differences between average body surface temperature (T_s, component parts: torso, 'T_{s_torso}'; bare gular skin, 'T_{s_skin}'; beak, 'T_{s_beak}') and air temperature (T_s-T_a) were calculated for the different regions of interest across the T_a gradient as well as the heat loss calculated in watts per body part. For all T_s except T_{s_beak}, I modelled T_s-T_a data using linear mixed models with Gaussian error distribution, T_a as the predictor variable and hornbill identity as a random factor. I split the T_{s_beak} -T_a dataset below and above the T_{s_beak} threshold T_a (lower beak and whole beak) and fitted linear mixed models with Gaussian error distribution to each of the two subsets, again with hornbill identity as a random factor, and T_a as the predictor. Linear mixed models were fitted by REML using R Studio interface (R Development Core Team, 2016) using package lme4 (Bates et al., 2015). Normality of all model residuals was confirmed visually using a Normal Q-Q plot (Kabacoff, 2011). Random terms were included in the model to account for the potential influence of repeated measures on the distribution of data. P-values < 0.05 were taken as statistically significant and mean estimates are reported ± 1 standard error (SE) unless otherwise stated.

5.4 Results

5.4.1. Sex-specific differences

Beak surface area is a sexually dimorphic trait in Southern Yellow-billed Hornbills (Figure 3). Initiation of panting behaviour occurred at T_a = 37.4 ± 2.1 °C (values are presented as mean ± SE, unless otherwise stated). I found no difference in T_a at panting initiation between males and females (Welch two sample t-test: t = -0.38, df = 9, p = 0.36).

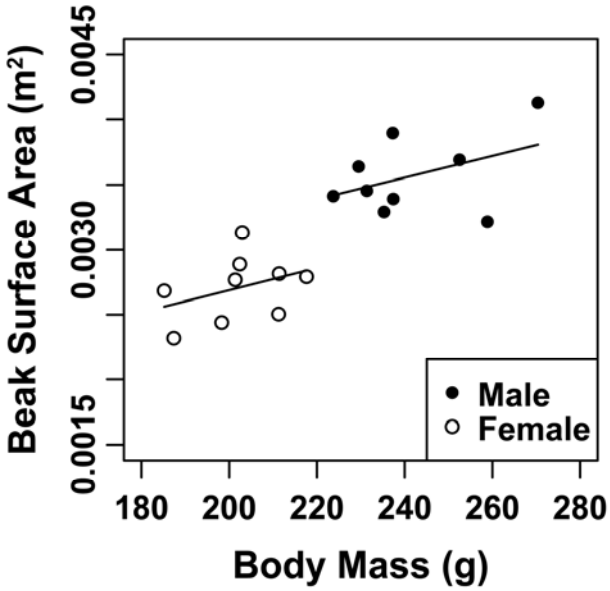

Figure 3 Beak surface area increases as a function of M_b in Southern Yellow-billed Hornbills. Data for nine males and nine females are shown.

5.4.2. Visual assessment of vasodilation

Back illumination of the hornbill beak revealed the presence of a network of fine blood vessels below the rhamphotheca in both sexes (Figure 4).

Figure 4 A lateral image of a female Southern Yellow-billed Hornbill with the beak backlit with a handheld flashlight, revealing the high degree of vascularity.

As the hornbills were subjected to the ramped profile of increasing T_a, the T_{s_beak} clearly changed in response to T_a (hereafter referred to as threshold T_a), indicated by a rapid change in the colour of the beak in 14 of the 18 study individuals, as visualised by the thermal imaging camera (mean threshold T_a ~30.7 °C, Figure 6).

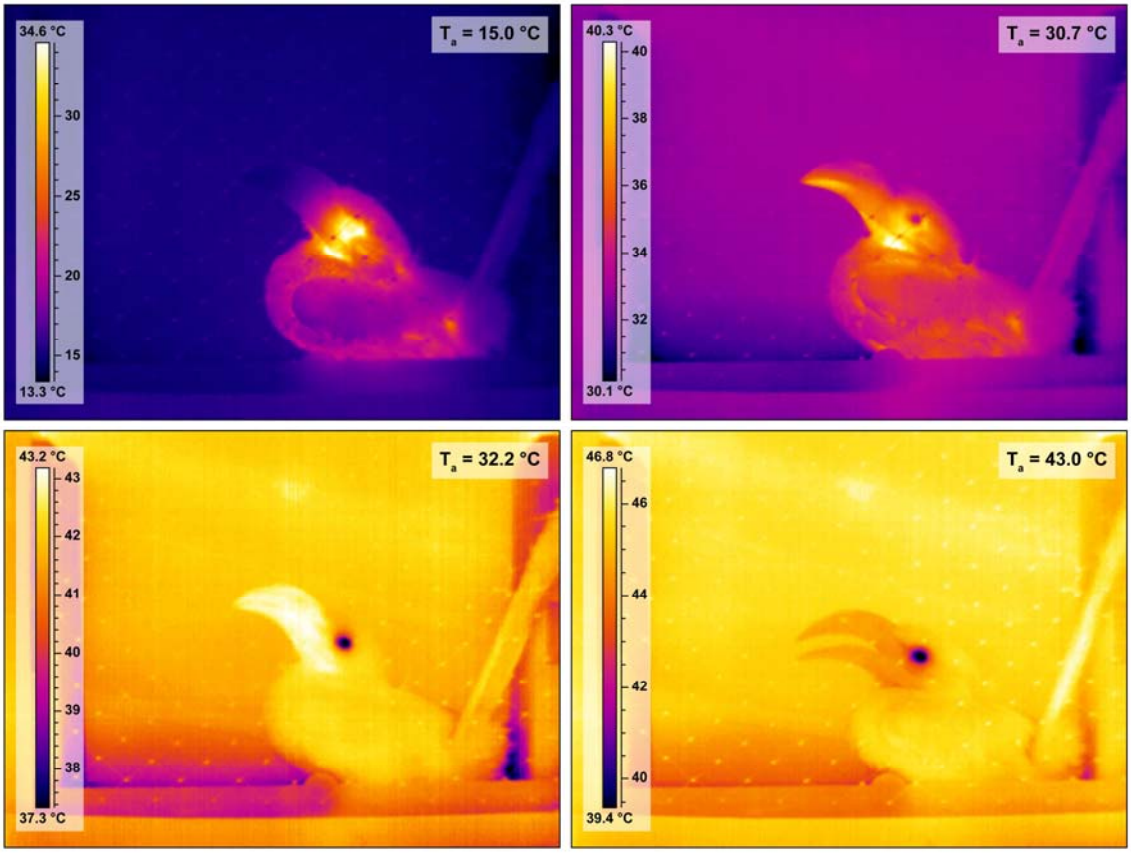

Figure 5 Thermal images of a female Southern Yellow-billed Hornbill at different T_as. Surface temperature (°C) is shown by the scale bar to the left of each image. Top left: the hornbill at T_a = 15 °C: beak surface temperature (T_{s_beak}) matches background T_s. Top right: the hornbill at threshold T_a = 30.7 °C, T_{s_beak} is changing, lower mandible first. Bottom left: the hornbill at T_a = 32.2 °C, note that T_{s_beak} is much higher than that of the rest of the body and the environment, indicative of heat being radiated from the beak. Bottom right: the hornbill at $T_a > T_b$ (T_a = 43 °C). The beak is cooler than the surrounding environment and the bird is using evaporative water loss to keep cool, as indicated by the open beak panting behaviour. Blue eye indicates passive evaporative heat loss.

5.4.3. Heat loss from the different body areas

As hypothesised, the relationship between T_{s_beak} and T_a differed markedly from that between T_{s_skin} and T_a and T_{s_torso} and T_a. As T_a increased from 15 °C to 45 °C, the difference between skin surface temperature and air temperature (T_{s_skin}-T_a) and the difference between torso surface temperature and air temperature (T_{s_torso}-T_a) decreased linearly (Figure 6; Table 2). T_{s_skin}-T_a was just under 30 °C when T_a was close to 15 °C. T_{s_skin}-T_a decreased linearly at a rate of 0.63 °C per 1 °C increase in T_a, as T_a approached T_b. At T_a = 45 °C, T_{s_skin}-T_a was below

0 °C (i.e. T_{s_skin} was cooler than T_a). The rate of change in T_{s_torso}-T_a with increasing T_a was much shallower (-0.11 °C per 1 °C increase in T_a); the maximum T_{s_torso}-T_a was 3.9 ± 0.2 °C at the lowest experimental temperature (~ 15 °C), likely due to the insulating properties of the feathers (Figure 6; Table 2).

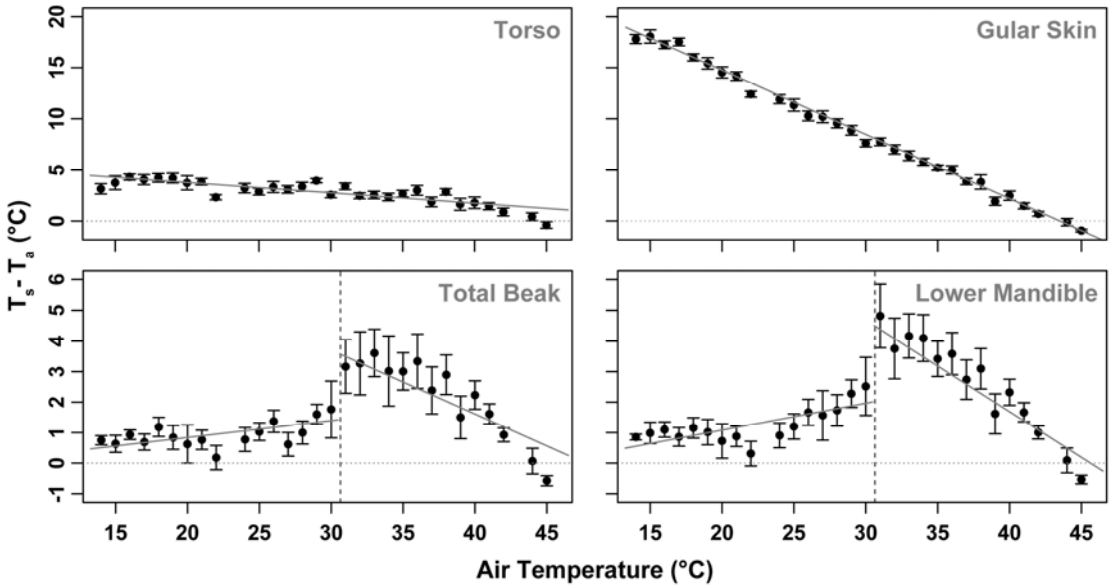

Figure 6 Difference between surface temperature and air temperature (T_s-T_a) plotted against air temperature (T_a) of the torso (T_{s_torso}), gular skin (T_{s_skin}), the beak as a whole (T_{s_beak}) and lower mandible of the beak in Southern Yellow-billed Hornbills. The dashed vertical line represents the T_{s_beak} threshold temperature. Error bars represent SE. Note that the scaling of the y-axes of the top two panels is different to that of the bottom two panels.

Table 2 The relationship between T_s-T_a (°C) and T_a (°C), estimates of effect sizes, standard errors (SE), 95 % confidence intervals (95 % CI) and t-values for Southern Yellow-billed Hornbills. Note the weak response of T_{s_beak}-T_a to increasing T_a at T_a < 30.7 °C, compared to the strongly negative response T_{s_beak}-T_a to increasing T_a at T_a > 30.7 °C, Linear mixed models were fitted with Gaussian error distribution and individual bird identity as a random factor.

Variable	Estimate (change in T_s-T_a per 1 °C increase in T_a)	SE	95% CI	t value
Torso (T_{s_torso})	-0.11	0.01	-0.12 - -0.09	-15.57
Gular skin (T_{s_skin})	-0.63	0.01	-0.65 - -0.62	-115.69
Beak (T_{s_beak}) < T_a 30.7 °C	0.06	0.02	0.03 - 0.10	3.50
Beak (T_{s_beak}) > T_a 30.7 °C	-0.24	0.04	-0.31 - -0.17	-6.93

n = 13 observations on 6 males and 8 females.

Although variable between individuals, T_{s_beak} -T_a was greatest at the threshold T_a at which the rapid change in T_{s_beak} occurred. The rapid change of T_{s_beak} was detectable in the lower mandible first at T_a = 30.6 ± 1.5 °C, followed by the upper mandible at T_a = 30.7 ± 1.0 °C (Figure 6). Although this sequence (lower mandible followed by upper mandible) was consistent across individuals, inter-individual variation in overall T_{s_beak} -T_a thresholds was

such that I could find no significant difference between the lower and the upper mandible with respect to the T_a threshold at which T_{s_beak} changed (Welch two sample t-test: t = -0.94, df = 31.94, p = 0.35). Below the T_{s_beak} threshold temperature, T_{s_beak} -T_a increased at a rate of 0.062 °C per 1 °C increase in T_a and at a rate of 0.002 W per 1 °C increase in T_a (Table 2; Table 3). At T_{s_beak} -T_a threshold T_a (~ 30.7 °C), T_{s_beak} -T_a was maximised and heat was radiated from the beak to the cooler environment with greatest efficiency. I found no difference in T_{s_beak} values between males and females at the threshold temperature (Welch two sample t-test: t = 0.61, df = 5.65, p = 0.57). As T_a increased above this threshold, T_{s_beak} -T_a declined at a rate of 0.24 °C per 1 °C increase in T_a. At the threshold temperature mean T_{s_beak} -T_a was 3.8 ± 0.6 °C and the mean heat dissipation from the beak was 0.1 ± 0.0 W: equivalent to 25.1 $W.m^{-2}$ (Figure 6).

Table 3 Heat dissipation (W) from different areas of the hornbill body as a function of T_a, estimates of effect sizes, standard errors (SE), 95 % confidence intervals (95 % CI) and t-values. Linear mixed models were fitted with Gaussian error distribution and individual bird identity as a random factor.

Variable	Estimate (change in heat dissipation (W) per 1 °C increase in T_a)	SE	95% CI	t value
Torso (T_{s_torso})	-0.024	0.003	-0.030 - -0.018	-7.365
Gular skin (T_{s_skin})	-0.002	0.000	-0.002 - 0.002	-63.000
Beak (T_{s_beak}) < T_a 30.7 °C	0.002	0.001	0.001 - 0.003	3.860
Beak (T_{s_beak}) > T_a 30.7 °C	-0.005	0.001	-0.008 - 0.002	-3.485

n = 13 observations of 6 males and 8 females.

5.4.4. Proportional heat loss

This mechanism of heat dissipation can only be effective over the range of T_a from threshold temperature up until $T_a \approx T_b$. At $T_a > T_b$ it is no longer possible for heat to be dissipated passively from the beak to the environment as the temperature gradient is reversed. Reflecting this, when $T_a > T_b$, $T_{s\_beak} - T_a$ became a negative value (Figure 6). Heat loss per unit surface area via the beak more than doubled at T_a > 30.7 °C (above the mean T_{s_beak} threshold) compared to T_a < 30.7 °C (Table 3). Maximum heat dissipation by the beak as a percentage of total body heat dissipation per individual was on average 8.0 % (range 1.4 – 19.9 %), and this occurred at mean T_a = 32.2 °C (range 18.0 – 39.4 °C) (Figure 7). The maximum percentage of heat loss via the beak was observed at T_a = 33.0 °C in one individual where the beak at that stage accounted for 19.9 % of total heat loss.

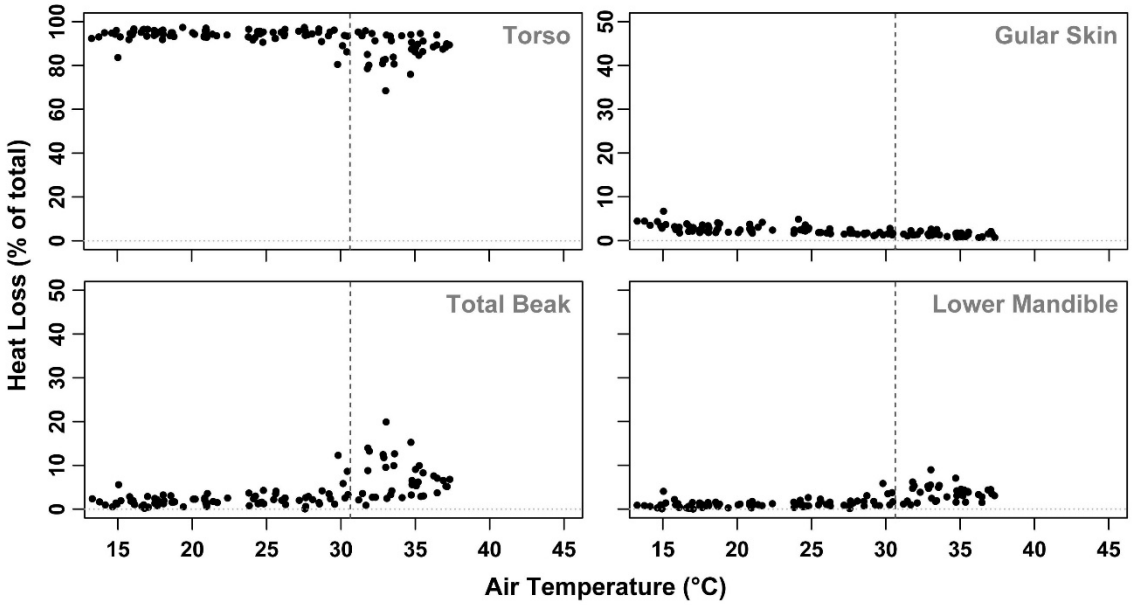

Figure 7 Heat loss as a proportion of total body heat loss (%) plotted against T_a of torso, gular skin, the beak as a whole and lower mandible of the beak in Southern Yellow-billed Hornbills. The dashed vertical line represents the T_{s_beak} threshold temperature. Data above the panting initiation temperature (T_a = 37.4 ± 2.1 °C) has not been included in this graph since evaporative heat loss has not been assessed and this makes total heat loss after initiation of panting incomplete.

5.5 Discussion

The data presented here confirm that hornbills, like toucans, can regulate heat exchange from their beaks, using them as thermal radiators when T_as are high, but restricting heat loss during cold ambient conditions. The large beaks of both hornbills and toucans are highly vascularised, and control of blood is regulated by vasoconstriction and vasodilation processes (Tattersall, 2016). Bird beaks contain branches of major cranial nerves (e.g. the trigeminal nerve) and associated sensory structures (Gutiérrez-Ibáñez et al., 2009; Cunningham et al., 2013a), which require a supply of oxygenated blood. Vascularity of the beak is therefore almost certainly a plesiomorphic avian trait (Schneider, 2005). Heat exchange from the beak occurs in all species investigated to date (Hagan and Heath, 1980; Hill et al., 1980; Scott et al., 2008; Tattersall et al., 2009; Symonds and Tattersall, 2010; Greenberg et al., 2012). The ability to regulate heat loss via the beak is probably most essential in large-beaked birds because of the need to conserve heat at low T_as (Symonds and Tattersall, 2010; Danner and Greenberg, 2015). These hornbill beaks therefore function as ‘thermal windows’ (Symonds and Tattersall, 2010), similar to better-known examples such as elephant ears (Weissenböck et al., 2010), bat wings (Reichard et al., 2010), lemur indices (Moritz and Dominy, 2012), dolphin fins (Noren et al., 1999; Williams et al., 1999), hummingbird eyes and axial region (Powers et al., 2015) and bird legs (Baudinette et al., 1976; Nudds and Oswald, 2007; Fitzpatrick et al., 2015). Hughes (2014)

suggested that the large beaks of toucans and hornbills evolved the ability to facilitate thermoregulation during hot weather conditions as an exaptation on top of foraging function. However, given the thermal constraints associated with heat loss from a very large beak in the cold, it is also possible that beak size and control over blood flow into the beak evolved in tandem under selective pressure to prevent heat loss during cold periods.

Although both hornbills and toucans have the ability to regulate the rate of heat exchange through their large beaks, the efficiency of this mechanism and the degree of control of T_{s_beak} differ markedly between the two species. For example, Tattersall et al. (2009) showed that adult Toco Toucans are able to adjust the rate of heat exchange from the beak in two distinct ways, increasing T_{s_beak} of either the proximal region (at $T_a \sim$ 20-25 °C), or of the entire outsized beak (at T_a > 25 °C), depending on T_a. In contrast, Southern Yellow-billed Hornbills in this study altered the T_s of the entire beak once T_as passed a threshold of ~30.5 – 31 °C. The sequence in which this occurred was the lower mandible immediately followed by the upper mandible. It is possible that the differences between species in the rate of change of T_{s_beak} may be explained by either physiological differences in vascular network or other differences in beak morphology, or differences in beak threshold temperature or heating rate of the chamber. Toco Toucans were able to dissipate on average 60 % of total heat loss via the beak (Tattersall et al., 2009). The heat dissipated via the beak in Southern Yellow-billed Hornbills was much less: on average ~ 8 % of total heat loss (maximum 19.9 % at T_a of 33.0 °C in one individual). This difference in contribution of the beak to overall heat dissipation between toucans and hornbills is partly explained by relative beak size, as the Toco Toucan's beak represents 30 - 50 % of total body surface area, whereas the Yellow-billed Hornbill's beak only represents 4.7 % of its total body surface area. However, dissipation of heat per unit beak surface area was also considerably lower in the hornbills compared to Toco Toucans. I calculated maximum rate per unit surface area using data presented in the figures in the paper by (Tattersall et al., 2009) and found that toucans dissipated as much as 204.8 $W.m^{-2}$ via their beaks, whereas the Yellow-billed Hornbills I studied only dissipated a maximum of 25.1 $W.m^{-2}$ via the beak. The reason for this large difference in efficiency of the heat dissipation mechanism is unclear, but could be linked to differences in the extent of the network of capillaries near the beak: a possibility that requires further investigation. A second explanation is that toucans allowed T_{s_beak} to rise at considerably cooler T_as than hornbills (20 - 25 °C compared to 30.5 – 31 °C) possibly due to acclimation to cooler temperatures or higher humidity in the chamber, discussed further below. This could have allowed them to achieve a steeper gradient between T_{s_beak} and T_a than hornbills, which should result in more rapid heat dissipation, all else being equal. A third explanation is the difference in the hardness of the rhamphotheca structure,

which is twice as high in hornbills as compared to toucans (Seki et al., 2010), potentially affecting thermal conductance and the efficiency in heat exchange (Andrade pers comm). This structural difference in beaks is likely associated with the foraging habits of the two species. In the Kalahari, hornbills use their beaks to break away pieces of tree bark and dig in the sand to find invertebrates, a foraging habit that requires a strong beak (Kemp, 1995), and is in contrast with beak properties of the soft fruit eating toucan (Ragusa-Netto, 2013).

In both the current study and the study of toucans by (Tattersall et al., 2009), a few individuals did not display dramatic changes in T_{s_beak} as T_a was increased. In the toucan study, these individuals were juveniles that did not appear to have the capacity to reduce T_{s_beak} at low T_as (Tattersall et al., 2009). I was unable to determine the age of my study individuals but all appeared to be adults (> 1 year of age (Kemp, 1995). Despite this, four individuals (out of 18 other than those removed early from the chamber) did not exhibit a rapid change in T_{s_beak} at any point during the trials: in these individuals, T_{s_beak} did not differ by more than 2.1 °C from T_a at any point during the entire experiment. I consider that the absence of T_{s_beak} change in these individuals could be a result of distress, since peripheral vasoconstriction has been observed in hens (*Gallus gallus domesticus*) in response to a minor discomfort trigger (Herborn et al., 2015).

Allen's rule (Allen, 1877) predicts a correlation between appendage size and temperature and / or latitude. Large appendages are likely to confer the greatest adaptive benefits, in terms of passive heat loss, to species living in hot environments (Greenberg et al., 2012; Campbell-Tennant et al., 2015; Danner and Greenberg, 2015). Hornbills and toucans are distributed across large areas of Africa, Asia and the Americas covering considerable ranges in climate conditions. It would be worth investigating whether within these families, cool climate hornbills and toucans have proportionately smaller beaks than those from hotter climates. One environmental factor that has received relatively little attention as a potential environmental correlate of beak size in birds is humidity. Many species of hornbills and toucans occupy habitats characterised by both high T_as and high humidity levels, conditions under which non-evaporative heat dissipation mechanisms are likely to be important. Because of the reduction in evaporative cooling efficiency associated with high water vapour pressures, the capacity to dissipate heat via non-evaporative avenues may, *a priori*, be expected to be under stronger positive selection in humid habitats. This leads to the prediction that thermal radiators such as beaks are more important for species inhabiting humid environments compared to those living in arid areas, an idea first proposed by Greenberg et al. (2012). This may provide an alternative explanation for the higher radiative capacity of the forest-dwelling Toco Toucan's beak when

compared to that of the arid savanna-inhabiting Southern Yellow-billed Hornbill. I suggest that further work on the physiology of heat dissipation through thermal windows, such as large beaks, should include species acclimated to different T_as as well as different humidity levels.

Southern Yellow-billed Hornbills breed during the hottest time of year (Austral summer: October to March). In Chapter 2, I found that panting behaviour severely impacts the foraging efficiency of males needing to provision their females and offspring in the nest as well as finding prey for themselves. These males increased their foraging effort on hot days, but at T_a exceeding the panting threshold temperature (34.5 °C) their prey capture success decreased by 41.9 %, and this appeared to be directly linked to panting behaviour (birds achieved lower prey capture rates when panting than not panting, at the same T_a, Chapter 2). Non-evaporative heat loss via the beak could therefore tremendously reduce the cost of heat dissipation between T_as of 30.7 °C (maximum T_{s_beak}) and 41.4 °C (normothermic T_b) by conserving water that would otherwise be lost via panting, and by allowing birds to maintain higher prey capture rates. I speculate that the large beak of Southern Yellow-billed Hornbills could therefore provide these birds with an efficient heat loss mechanism that is advantageous to their foraging and reproductive performance in hot environments.

I found no difference in proportional efficiency of non-evaporative heat loss between male and female hornbills. Female hornbills have been observed to extrude their beaks out of the nest opening during periods of high T_a. Besides the potential of lowering nest temperature by panting outside the nest, these females could make use of convective cooling as air flows past and promotes radiative heat loss via the beak. I suggest that future research should focus on the importance of this non-evaporative heat loss mechanism to females confined to the nest cavity, as this could be a strategy for the females to influence the microclimate in the nest box.

5.6 Conclusions

My data add to a growing body of literature revealing the importance of the avian beak in thermoregulation (Hagan and Heath, 1980; Tattersall et al., 2009; Symonds and Tattersall, 2010; Greenberg et al., 2012; Burness et al., 2013; Luther and Greenberg, 2014; Danner and Greenberg, 2015). The capacity for controlled radiative heat exchange via the beak in hornbills appears to be most efficient at T_as within ~ 10 °C below T_b. Although heat loss via the beak has been investigated in diverse avian species (Hagan and Heath, 1980; Greenberg et al., 2012; Burness et al., 2013), the capacity to regulate rates of heat dissipation has so far been demonstrated only in the Toco Toucan (Tattersall et al., 2009) and the Southern Yellow-billed Hornbill (current study). Beak size in birds is correlated with latitude and T_a (Symonds and

Tattersall, 2010). However, in addition to these I argue that water vapour pressure (and hence the humidity gradient available for evaporative heat loss) in the bird's habitat, likely gives rise to selection pressure acting on beak size, maximising capacity for radiative heat loss in situations where evaporative cooling is likely to be inefficient. Therefore, I speculate that Allen's rule (Allen, 1877) may apply to humidity gradients as well as temperature gradients: large appendages should be particularly advantageous to birds as well as mammals inhabiting hot, but also humid climates.

CHAPTER 6 THE INFLUENCE OF TEMPERATURE AND RAINFALL ON HORNBILL REPRODUCTIVE SUCCESS

6.1 Abstract

In the previous chapters I investigated the mechanisms linking high air temperatures (T_as) to changes in hornbill reproductive success. Rainfall is also well known to be an important factor determining reproductive success in arid-zone birds, mainly through its effects on food abundance and the timing of breeding. In this chapter I aim to test how T_a as well as rainfall affect hornbill breeding success at an annual scale, by comparing the results of my current study with the results of a preceding study (austral summers between 2008 – 2011) carried out on the same population of Southern Yellow-billed Hornbills (*Tockus leucomelas*).

Hornbill reproductive success was higher during the first study (2008 – 2011), than during my subsequent study (2012 – 2015), despite the same number of artificial nests being monitored in both studies. Long-term weather records from the Van Zylsrus weather station (South African Weather Service; ~ 30 km from the study site) showed an increase in the number of days per year that T_{max} exceeded the hornbill 50 % panting threshold temperature (34.5 °C) between 1995 and 2015. Temperatures were milder and rainfall was higher during the three breeding seasons of the first study with warmer cold extremes and cooler hot extremes than during my current study. Rainfall during the breeding season had a positive effect on the total number of breeding attempts, but no effect on mean clutch size per season. Overall, reproductive output (number of chicks fledged per nesting attempt) of hornbills was higher during the first study compared to the current study. My mechanistic data suggest this is likely to be linked to the milder climatic conditions during the first study.

In the previous chapters I showed how high maximum air temperature (T_{max}) during the nesting period impacted nesting success through decreases in male provisioning, reduction of female body condition and reduced chick growth. My findings suggest rainfall is also important, as the number of hornbill breeding attempts per season increases with rainfall during the nesting period. Weather data confirm that conditions in the Kalahari are becoming increasingly unfavourable for breeding hornbills, as shown by annual increases in the number of days on which T_{max} exceeds the hornbill panting threshold temperature. In keeping with this, data collected over six breeding seasons between 2008 and 2015 suggest a decline in hornbill reproductive success over this period. Future predicted weather scenarios could therefore lead to a population decline of Southern Yellow-billed Hornbills in this region of the Kalahari.

6.2 Introduction

Desert ecosystems are often characterised by extreme high air temperatures (T_as) in summer, high levels of solar radiation and unpredictable precipitation. Under such harsh conditions, breeding attempts in many desert-dwelling avian species are most pronounced after rainfall events (Maclean, 1969). This allows them to take advantage of influxes of primary production and arthropod abundance (Dean and Milton, 2001). Such breeding systems are likely to be highly vulnerable to changes in the timing and amount of rainfall associated with climate change. For example, if rain falls early in the summer season then the high T_as that follow during mid-summer can still negatively impact arthropod abundance, however if it falls late then food might be available throughout the winter months and favour the birds' body condition at the onset of the next breeding season (Maclean, 1969). Resident birds in the Kalahari undertake fewer breeding attempts during low rainfall conditions and have a lower reproductive success (Dean et al., 2009). Complete absence of breeding attempts by birds have been reported in response to low rainfall, potentially as a result of low arthropod abundance (Poulin et al., 1992).

The Southern Yellow-billed Hornbill (*Tockus leucomelas*) breeding season in southern Africa coincides with rainfall in the austral summer (Kemp, 1995). At my study site, rain falls within the months November to April (Kuruman River Reserve [KRR] weather station 2009 – 2016). Multiple studies on the *Tockus* genus have revealed that hornbills in arid environments start breeding after the first pronounced rainfall, presumably to secure food availability for nestlings (Kemp and Kemp, 1972; Diop and Treca, 1996; Stanback et al., 2002; Klaassen et al., 2003; Finnie, 2012). Hornbill chicks within the sealed nest cavity are relatively safe from predators, suggesting that breeding success is primarily dependent on either male provisioning effort or internal factors in the nest (Moreau and Moreau, 1941). The trade-offs made by hornbill males on hot days in my study resulted in foraging efficiency declining with increasing T_as (Chapter 2). At the same time, high T_as almost certainly increased requirements for evaporative cooling for the entire hornbill family and the need for food to replenish lost body water content. This mismatch between food provided by male hornbills and food required by female hornbills in the nest, potentially explains the cannibalism of eggs and nestlings by female hornbills observed by Finnie (2012), Chan et al. (2007), Ng et al. (2011) and the current study (Chapter 4), as well as partly explaining the association between high T_as and nest failures I observed even in cases without cannibalism (Chapters 3 and 4). In a contrasting scenario, Mills et al. (2005) observed high provisioning rates by males and prey items left uneaten in the nests during a breeding season with exceptionally high rainfall.

The effects of current warming trends on the breeding success of Southern Yellow-billed Hornbills have not been rigorously examined yet. However, a long-term study on White-plumed Honeyeaters (*Ptilotula penicillatus*) living in an arid environment demonstrated that increases in the frequency of low rainfall seasons and high T_as can reduce parental body mass (M_b) and even lead to adult mortality (Gardner et al., 2016). In hornbills, Mills et al. (2005) suggested that low body condition of the females can result in early abandonment of the nest which will have repercussions on the fledging success of the chicks, a pattern confirmed in Southern Yellow-billed Hornbills (Chapter 4).

The aim of this thesis was to investigate specifically the impacts of high T_{max} on Southern Yellow-billed Hornbills during the reproductive period. In the previous chapters I elucidated the mechanisms by which high T_as affect the reproductive performance of a population of this species in the southern Kalahari at the Kuruman River Reserve (26°85' S, 21°49' E). I concluded that foraging success of breeding male hornbills was compromised by panting behaviour and changes in microsite use at T_as above 34.5 °C (Chapter 2). This reduction of prey items caught during hot periods during the day affected both the males' own food intake, with implications for his M_b maintenance, and the number of prey items provisioned to the nest (Chapter 3). Increased daily maximum air temperature (T_{max}) and reduced biomass provisioning (affected by T_{max}) both had a negative effect on female M_b and chick growth during the nesting period, ultimately influencing fledging success and the size and mass of fledglings (Chapter 4).

Because of the close relationship between temperature and physiological processes, and the non-linear relationships between T_a and physiological methods of thermoregulation (Scholander, 1955), T_a can be expected to have a profound impact on the performance of birds and other organisms. However, besides T_a, rainfall is another external climatic factor affecting reproductive performance in birds. As described above, in desert environments, rainfall is commonly associated with increases in food availability (Dean and Milton, 2001; Illera and Díaz, 2006), therefore affecting the body condition of parents prior to breeding and the associated optimal timing of breeding attempts (Drent and Daan, 1980). Increased T_as and lower rainfall are predicted for the southern Kalahari under climate change, and recent weather trends are beginning to bear these predictions out (Kruger and Sekele, 2012). The existence of a previous study including data on the breeding success of the population of hornbills at my study site during previous years (2008 – 2011) (Finnie, 2012), provides an excellent opportunity to compare breeding success of Southern Yellow-billed Hornbills over a short time scale (n = 6 years).

The aim of this chapter was to compare reproductive success between two studies of the same population of Southern Yellow-billed Hornbills (the first study by Mike Finnie, 2008 – 2011, Finnie 2012; and the current study 2012 - 2015) and test whether a) climatic impacts on breeding success are already visible over a short time scale (2008 – 2015) and b) how T_a and rainfall affect breeding success at annual and local population. I first aimed to assess whether climatic conditions were indeed different during the nesting seasons of the first study (2008 – 2011; Finnie 2012) and the nesting seasons of the current study (2012 – 2015) by comparing minimum and maximum T_as as well as rainfall. I hypothesised that rainfall could have an effect on the number of hot days during the hornbill breeding season, since rainfall promotes land surface cooling. Through changes in breeding conditions (i.e. food availability and frequency of hot days), rainfall was also predicted to affect the total number of breeding attempts per season and the number of eggs laid per breeding attempt. Furthermore, I predicted that rainfall and T_a, via influences on food availability and thermoregulatory trade-offs, would affect female body condition while in the nest as well as the number of chicks fledged per successful breeding attempt.

6.3 Methods

6.3.1. Study site and population

Mike Finnie (PhD, Clare College, Cambridge University, United Kingdom) started working with the study population of Southern Yellow-billed Hornbills in 2008 at the Kuruman River Reserve (26°85’ S, 21°49’ E). The hornbills are individually identifiable by a combination of three colour rings and a SAFring coded metal ring fitted on their tarsi. A total of 47 artificial nest boxes were placed in 2008 within hornbill territories identified by Finnie (Finnie, 2012). Due to Finnie’s efforts, the hornbills are semi-habituated and readily use the nest boxes provided for breeding. Hornbill breeding success was monitored during seven summer breeding seasons (2008 – 2016, excluding summer season 2011 / 2012) by either Finnie (first study 2008 - 2011) or me (current study). Breeding success across seasons could be compared because the same number of boxes (n = 47) were monitored each season.

Reproductive output was quantified using “nesting success” (a binary variable whereby successful nesting attempts were defined as those which successfully fledged at least one chick); and via the number of successfully fledged chicks per nesting attempt. A nesting attempt was logged when a female hornbill spent at least one day in a nest with a sealed entrance. The study by Finnie recorded 67 nesting attempts from 2008 to 2011 and the current study from 2012 to 2015 recorded 43 nesting attempts in the 47 nest boxes. The boxes were

also monitored by an assistant in the summer season 2015 / 2016 and no breeding attempts were recorded during that summer. For a full description of the study site and population see Chapter 1.

6.3.2. Weather data

In order to compare the impact of rainfall and T_a during the first hornbill study (2008 – 2011) with that of the current hornbill study (2012 – 2015); weather data were required for the entire period. Weather data were obtained from two weather stations erected at the study site. These were the 'Meerkat' weather station (owned by Cambridge University and data accessed with permission from Prof T.H. Clutton-Brock, data available 2009 – 2016) and the 'Hot Birds' weather station (supplied by the University of Cape Town for the hornbill project, data available from 2012 – 2016) (Vantage Pro2, Davis Instruments, Hayward, U.S.A.). 'Meerkat' and 'Hot Birds' weather stations were situated within ~ 5 km of each other at the study site. Datasets from these two stations were matched in terms of date and time for the period of overlap (2012 - 2016), and the average of the two recordings for each date and time (presented as 'KRR") were used for analyses. Longer term weather data (1995 – 2015) were available from the Van Zylsrus weather station situated in the town of Van Zylsrus, ~ 30 km from the study site (owned by the South African Weather Service [SAWS], data were used with permission from Dr Andries Kruger, SAWS). Weather data from the KRR weather stations were used by preference where possible (ie post 2009), since these data were collected at the study site and therefore more accurately reflect conditions there.

6.3.3. Rainfall compared between KRR and Van Zylsrus

Rainfall recorded by the two weather stations at the KRR study site between December 2009 and March 2011 differed markedly from rainfall recorded by the Van Zylsrus weather station during this period. For example, cumulative rainfall at the study site between December 2009 and March 2011 was 712.6 ± 17.4 mm and only 214.2 ± 9.1 mm of rain was recorded in Van Zylsrus in that period. Rainfall patterns in the Kalahari are localised due to convective thunderstorms (Porporato et al., 2003) and have a large impact on vegetation growth in the region (Sporton and Thomas, 2002). The Normalized Difference Vegetation Index (NDVI) obtained from satellite images has been successfully used to produce estimates of rainfall in the Kalahari and NDVI generally tends to lag behind rainfall by 1 to 2 months (Grist et al., 1997). The annual NDVI for the hornbill study site shows a good fit with the annual rainfall recorded by the KRR weather station (1999 – 2016, $R^2 = 0.63$, $p < 0.001$) (D. Gaynor unpublished data). Rainfall data from the Van Zylsrus weather station were used to assess

rainfall during the 2008 / 2009 and 2009 / 2010 seasons when weather data were missing for KRR site. These were likely to underestimate the actual rainfall at the study site based on NDVI data. Therefore, I was confident to interpret that rainfall was higher during the months of the first hornbill study (2008 – 2011) as compared to the current study.

6.3.4. Hornbill panting threshold temperature

In Chapter 2, I identified a threshold T_a (34.5 °C) at which the male hornbills spent 50 % of their time performing heat dissipation behaviour (panting), which I calculated following the methods of (Smit et al., 2016) (Figure 1). This temperature threshold value was used to differentiate between cool days T_a < 34.5 °C and hot days T_a > 34.5 °C. Using this definition of a "hot day", I assessed whether the number of hot days had increased since 1995, and whether there was any correlation between rainfall and the number of hot days per summer breeding season.

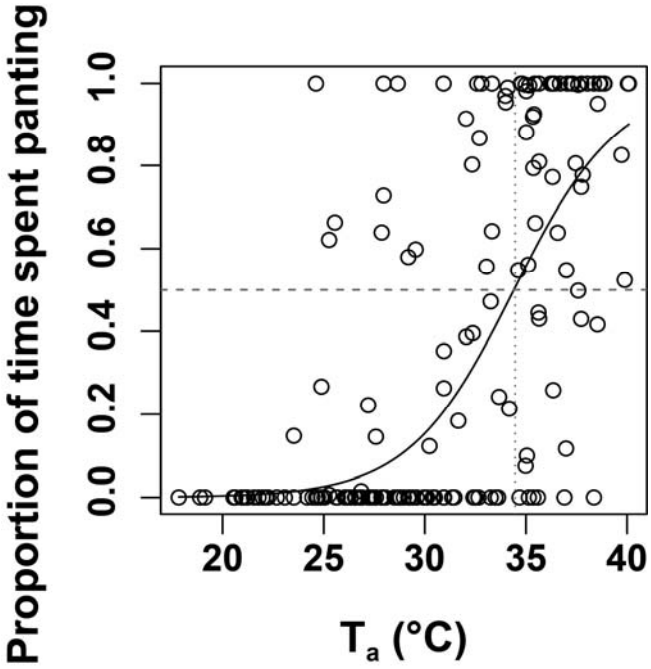

Figure 1 The proportion of time spent panting (heat dissipation via respiratory evaporative heat loss) as a function of T_a in male Southern Yellow-billed Hornbills. The black line represents a logistic regression with a binomial error distribution that includes the variable T_a. Individual ID nested in season was included as a random factor. At T_a = 34.5 °C, individuals spent on average 50 % of their time panting as indicated by the grey grey dashed lines. Data were derived from 204 focal observations collected from 12 males across three breeding seasons.

6.3.5. Linking timing of breeding with climate

The period between the first female of the season to enter the nest and the last chick to fledge was important in identifying relevant time windows for climate data. Rainfall at the study site is

known to have a lagged effect on prey abundance for small carnivorous mammals and birds (Doolan and Macdonald, 1997). Therefore, rainfall prior to the birds entering the nest and during the nesting period could influence food availability. In recognition of this, rainfall during a two-month period prior to nesting is commonly used as a proxy of food availability during that breeding attempt for birds in Kalahari ecosystems (Ridley and Raihani, 2007). Therefore I have also used this two-month window of rainfall in relation to analyses of nesting success and the number of nesting attempts in this chapter. Mean T_{max} between hatching of the first chick and fledging of the last chick influenced aspects of parental behaviour and reproductive success (Chapter 3 and 4). In the current chapter, the period between the first female hornbill of the season to enter the nest and the last chick to fledge is referred to as the 'nesting period'. The average length of the nesting period during each of the three breeding seasons of the current study was 109.0 ± 10.6 days. The first date that a female entered the nest was 10 November in both 2012 / 2013 and 2014 / 2015, and was slightly earlier (28 October) in 2013 / 2014 (Figure 2).

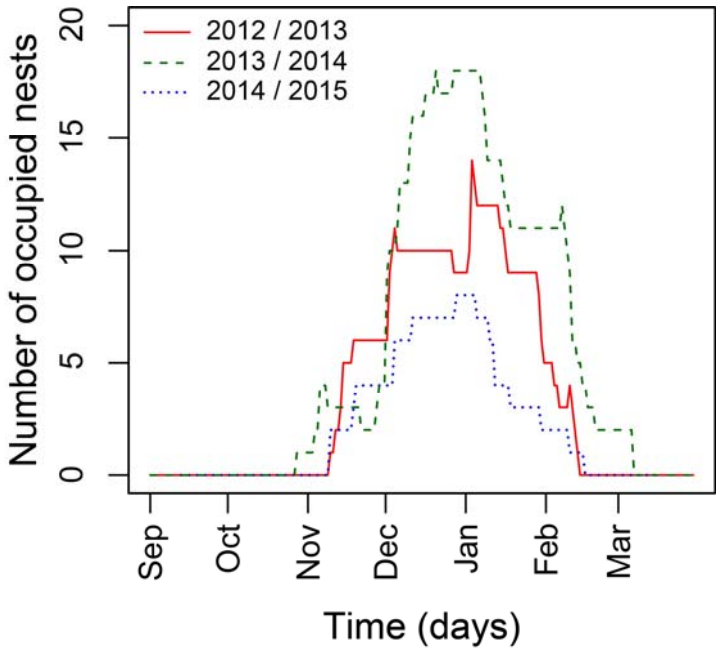

Figure 2 The number of occupied nests as a function of time of the year (days), showing the timing of breeding of Southern Yellow-billed Hornbills at the study site during the current study (2012 – 2015).

6.3.6. Use of non-correlative rainfall data to predict timing of breeding

Finnie (2012) stated that during his study, 91 % of the hornbill pairs attempted breeding within 20 days of the first notable rain event (> 10 mm). He therefore concluded that timing of breeding in hornbill pairs was correlated with rainfall. Due to the lack of availability of exact dates of

breeding attempts by hornbills during the first study (2008 to 2011), I assumed that nesting periods between 2008 and 2011 took place over 109 days (matching the mean length of the nesting period of hornbills in the current study) after the first day of notable rainfall (> 10 mm) in the summer season. This method was conservative with respect to calculation of the amount of rainfall prior to breeding attempts as it only included the first notable rain event of each season and therefore could only have underestimated rainfall two months prior to nesting during the first hornbill study.

6.3.7. Female body condition

Females nesting in boxes were weighed on a top balance with a resolution of 0.01 g (MXX-612, Denver Instruments, Germany) at a weekly interval during incubation and twice daily (within 1-hour after sunrise and within 1-hour before sunset) after the chicks had hatched. The tarsus length was measured to the nearest 0.1 mm from the notch of the intertarsal joint at the back of the bird's leg to the point where the foot bends with digital calipers (SDC150, Scangrip, Denmark). Female body condition was calculated as mean daily M_b divided by the tarsus length cubed ($g.mm^{-3}$) (Finnie, 2012).

6.3.8. Statistical analyses

All analyses were conducted in the R statistical environment using R Studio interface (R Development Core Team, 2016). For analyses of weather and breeding data, I used Student's t-tests, a Fisher's exact test (for breeding success only, see below), and Generalised linear models (GLM) and linear models (LM). GLMs and LMs were computed using the lme4 package (Bates et al., 2015) and the MuMin package was used for model selection and averaging (Bartoń, 2015). I constructed global models that consisted of all the variables I hypothesised to have an effect on the response variable. Best-fit models were chosen based on comparison of the corrected Akaike Information Criterion (AICc) between all possible nested models within the global models, using the "dredge" function in MuMin. Goodness of fit to model assumptions was assessed with residual plots, and results from all models with ΔAICc < 2 were presented. I used model averaged estimation of effects, standard errors and p-values when the set of best-fit models (within ΔAICc < 2) contained more than one model. Random terms were not implemented because for each variable I only had one value, being the average from multiple individuals per breeding season. Prior to fitting global models, linear regression was used to check for collinearity of the predictor variables and correlated variables were never included in the same model. For example, weather variables mean T_{max} (during the nesting period), rainfall (during the nesting period), pre-breeding rainfall (two months before the nesting period), mean

T_{max} during the winter season (May – August), and rainfall during the winter season (May – August) were not correlated and therefore could be fitted in the same models. Error bars plotted in the weather data and female body condition graphs all represent 1 SE. P-values < 0.05 were taken as statistically significant and mean estimates are reported ± 1 standard error (SE) unless otherwise stated.

Weather data comparison

No weather station was present at KRR during the 2008 / 2009 breeding season (first study), therefore I compared weather data from the KRR and Van Zylsrus weather stations to validate the use of Van Zylsrus weather data as a proxy for T_a and rainfall at the study site during the 2008 / 2009 breeding season. The averaged weather data obtained from the onsite weather stations (KRR) were used as the response variable to the predictor variable long term weather data (Van Zylsrus). A linear model was fitted to test the correlation between the KRR and Van Zylsrus weather stations. The data were plotted separately for daily minimum air temperature (T_{min}), daily T_{max} and rainfall. The intercept, slope estimate and R squared value of the model fit are presented.

Historical increase in air temperature

The number of days per year that were above the panting threshold temperature (34.5 °C; Figure 1) were calculated using the long-term Van Zylsrus weather data (1995 – 2015) and the temporal trend was modelled using a GLM with a Poisson error structure. The years 1999 - 2000, 2002 - 2004, 2006, 2009 - 2010, 2012 were excluded from this analysis because in these years more than 5 % of the weather data were missing.

Thermal conditions during the hornbill nesting seasons

The mean daily T_{min} and mean daily T_{max} during the nesting period (November to March) of Southern Yellow-billed Hornbills were compared between the first study (2008 – 2011) and the current study (2012 – 2015) using a Student's t-test, in order to test for differences between breeding conditions during the two studies.

Rainfall during the hornbill breeding season (September – March)

Cumulative rainfall during the breeding season (September to March) of Southern Yellow-billed Hornbills was compared between the first study (2008 – 2011) and the current study (2012 – 2015) using a Student's t-test, in order to test for differences between breeding conditions in terms of rainfall during the two studies. Rainfall data were used from both the KRR and Van

Zylsrus weather stations, to assess how missing data from the KRR weather stations in the 2008 / 2009 breeding season affected records of cumulative rainfall during the first study (2008 – 2011).

Relation between hot days and rainfall

Rainfall was hypothesised to affect the number of hot days per month during the nesting season. A GLM with a Poisson error structure was used to test for a relationship between the number of days per month that T_a exceeded 34.5 °C and monthly rainfall. Monthly weather data were derived from the KRR stations during the nesting period (November to March) of the years 2009 – 2015. Only the months that had less than 5 % missing data were included in this analysis.

Intensity of breeding in the current study

The number of occupied nests during each day of the season were not available for the first study (2008 – 2011) on this hornbill population. In order to understand how the number of occupied nests was related to rainfall and T_{max}, daily data for each of these three variables were plotted in a graph each for season 1 (2012 / 2013), season 2 (2013 / 2014) and season 3 (2014 / 2015) of the current study. The x-axis represents the first date being two months before the first female went into the nest and the last date being one month after the last chick fledged from the nest. Cumulative rainfall (mm), mean T_{max} (°C), and total number of occupied nests were each plotted on their own y-axis per graph to aid visual understanding of relationships between these variables.

Effect of climatic variables on the total number of breeding attempts per season

A GLM with a Poisson error structure was used to test for a relationship between the total number of breeding attempts per season as a function of the predictor variables mean T_{max} (during the nesting period), rainfall (during the nesting period), pre-breeding rainfall (two months before the nesting period), mean T_{max} during the winter season (May – August) and rainfall during the winter season (May – August). In order to compare the data between seasons, only breeding attempts observed in nest boxes (and not those in natural cavities) were used in this analysis. Sample size for these models included a total of 67 breeding attempts reported in the study by Finnie between 2008 and 2011 and 43 attempts from the current study between 2012 and 2015. In his study, Finnie (2012) did not report on the exact nesting periods of the hornbills, but mentioned that all but three females entered the nest after the first noticable rainfall. The first rainfall of 2008 / 2009 was 18.2 mm on 26/10/2008; of

2009/2010 was 12.8 mm on 11/10/2009 and of 2010 / 2011 was 17.4 mm on 18/11/2010 therefore these dates were taken as estimates of breeding starting dates for the first study (2008 – 2011). Length of the nesting period for each of these three years was assumed to be 109 days (in keeping with the mean annual length of the nesting period recorded in the current study, as described above). No nesting attempts were made during the breeding season of 2015 / 2016. In order to include these data in the analysis, the nesting period of 2015 / 2016 was hypothesised to start on 27/11/2015 after a single rainfall event of 11.6 mm and to continue for 109 days from this date.

Effect of climatic variables on mean clutch size per season

A LM with a Gaussian error structure was used to test for a relationship between mean clutch size per season as a function of the predictor variables mean T_{max}, rainfall (during the nesting period), pre-breeding rainfall (two months before the nesting period; September and October), mean T_{max} during the winter season (May – August) and rainfall during the winter season (May – August). Data were derived from six breeding seasons between 2008 and 2015, but did not include the 2015 / 16 breeding season (no breeding attempts recorded).

Female body condition

Female body condition as a function of the number days spent in the nest was compared between the two studies (2008 – 2011 versus 2012 – 2015) to see whether differences in T_a and rainfall during the studies affected female body condition. Female body condition was plotted as a polynomial regression fit with error bars and compared visually. Data were available from two breeding seasons during the first study (2009 – 2011), and derived from 36 females during 41 breeding attempts. During the current (second) study, data were available from 22 females during 38 breeding attempts during three breeding seasons between 2012 – 2015.

Reproductive output

The proportion of successfully fledged nests was compared between the two studies (2008 – 2011 versus 2012 – 2015) with a Fisher's exact test for count data. Reproductive output of the two studies was compared in terms of the mean number of chicks that successfully fledged per breeding attempt with a Student's t-test (the number of fledged chicks was not available per season from the first study and therefore only the totals per study could be compared). Data were derived from 67 breeding attempts recorded between 2008 and 2011 with a total of

38 chicks fledged and of 43 breeding attempts recorded between 2012 and 2015 with a total of 17 chicks fledged.

6.4 Results

6.4.1. Van Zylsrus and KRR weather data

T_a data from the two locations (Van Zylsrus and KRR) were closely correlated when assessing the variables daily T_{min} and daily T_{max}, although Van Zylsrus recorded slightly warmer T_as (approx. 1°C) in general. Correlations were close enough to provide confidence that Van Zylsrus T_a data could be used as a proxy for T_as at the study site during the 2008 / 2009 breeding season when no weather station was present at KRR. However, daily rainfall patterns differed widely between the two locations (Table 1; Figure 3).

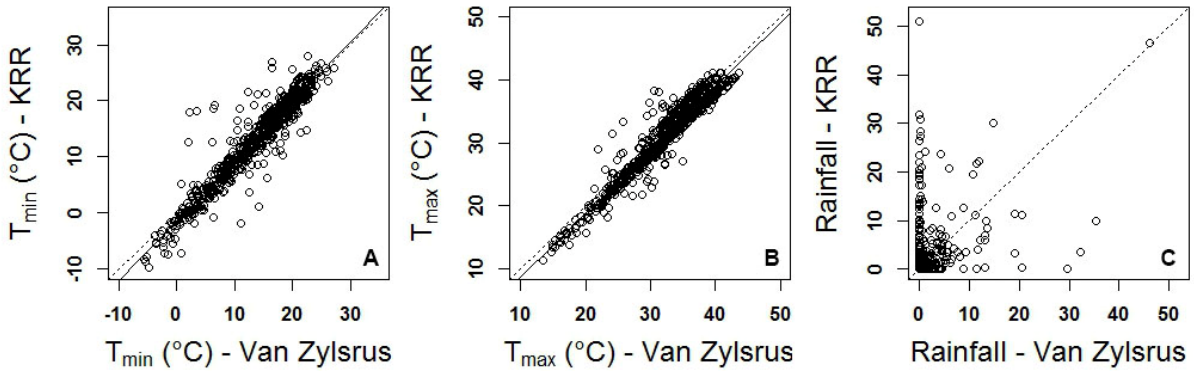

Figure 3 Comparison of daily T_{min} (A), daily T_{max} (B) and rainfall (C) between the weather stations at KRR and at Van Zylsrus. The black line represents the model fit and the dotted line is the ideal fit (1:1). Data were derived from the years 2010 – 2015.

Table 1 Estimates of the intercept, the slope and the multiple R-squared value of the linear relationship of the T_{min} and T_{max} as measured by the stations at KRR and the Van Zylsrus weather station. The slope estimate refers to the change in KRR T_a per 1 °C increase in T_a as measured by the Van Zylsrus weather station and is very close to 1. Intercept and slope estimates are not provided for rainfall, because of the lack of correlation.

	Intercept	Slope estimate	Multiple R^2
T_{min}	-1.398	1.06	0.90
T_{max}	-1.494	1.01	0.93
Rainfall	-	-	0.18

6.4.2. Historical increase in air temperature

The number of days per year that T_a exceeded the hornbill panting threshold temperature (34.5 °C) increased significantly between 1995 and 2015 (GLM estimate = 0.018 ± 0.004, t = 4.46, p < 0.001) (Figure 4).

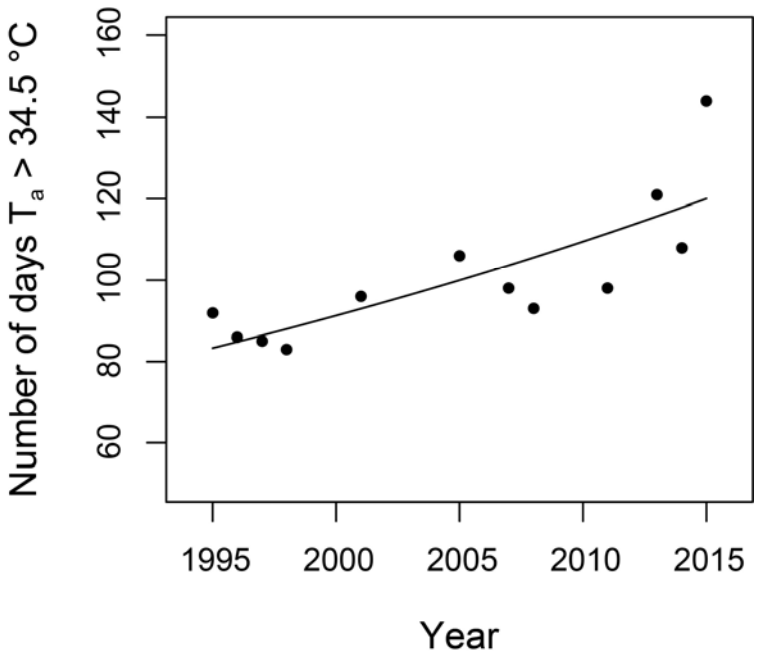

Figure 4 Number of days per year that T_a was above the Southern Yellow-billed Hornbill panting threshold temperature (34.5 °C; 1995 – 2015; Van Zylsrus weather station data). The black line represents the general linear model with a Poisson error structure.

6.4.3. Thermal conditions during the hornbill nesting period (November – March)

Overall, conditions during the nesting periods of 2008 – 2011 were milder with warmer cold extremes and cooler hot extremes than during the 2012 – 2015 nesting periods. Daily T_{min} was significantly higher in the nesting periods of 2008 – 2011 as compared to 2012 – 2015 (first study: 15.1 ± SD 6.3 °C; current study: 8.1 ± SD 6.7 °C; t = 14.57, p < 0.001; Figure 5A) and daily T_{max} of 2008 – 2011 was significantly lower as compared to the nesting periods of 2012 – 2015 (first study: 34.5 ± SD 3.6 °C; current study: 35.2 ± SD 4.0 °C; t = -2.58, p = 0.005; Figure 5B).

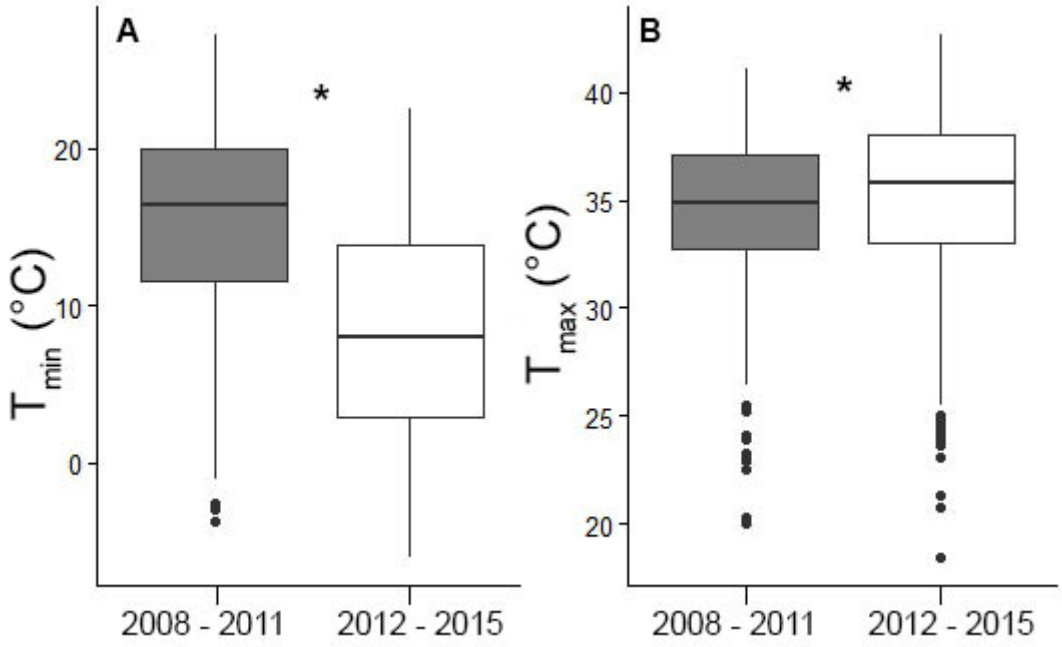

Figure 5 (A) Daily T_{min} (°C) and (B) daily T_{max} (°C) during the nesting periods (November - March) of the first (2008 – 2011) and the current (2012 – 2015) study on Southern Yellow-billed Hornbills. Error bars represent the standard error and asterisks denote significant difference.

6.4.4. Rainfall during the hornbill breeding season (September – March)

Variation between weather stations in rainfall recorded was high, due to patchy manner in which rain falls in the Kalahari (localised thunderstorms; Tyson and Crimp (1998). Cumulative rainfall during the breeding seasons (September – March: inclusive of the two-month period prior to the first female entering the nest) of the years 2009 – 2011 was much higher at KRR than during the breeding seasons of the years 2012 – 2015, although this was not the case at Van Zylsrus. This is despite the fact that fewer months of data were available from KRR for the first study than for the second – hence the first study period may have received more rainfall than the graph implies. Cumulative rainfall during the first study (2008 – 2011) was significantly higher than during the current study (2012 – 2015) as measured by the KRR weather station location ($t = 3.03$, $p < 0.003$; Figure 6).

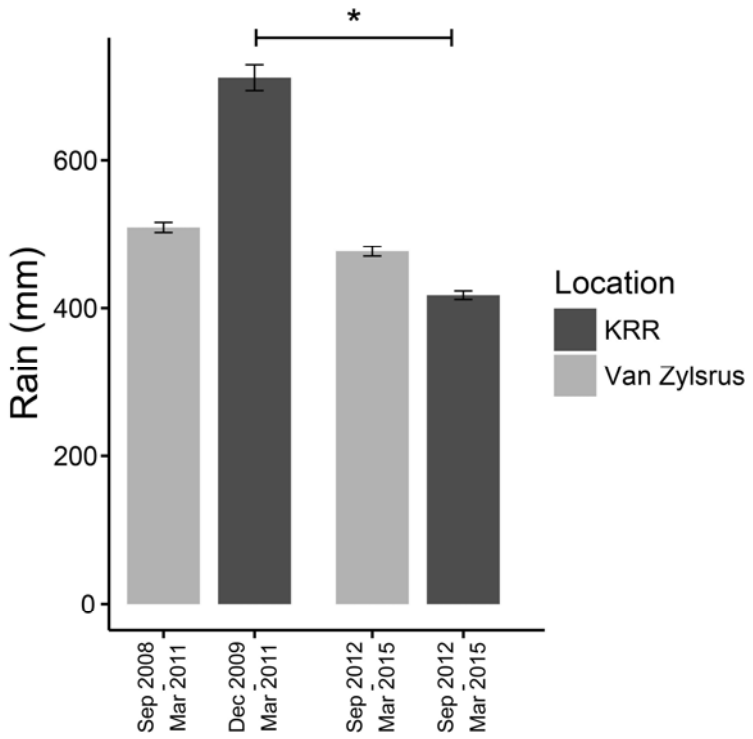

Figure 6 Total rainfall (mm) for the study period 2008 - 2011 and 2012 - 2015. Weather data of the KRR station were only available post-December 2009. Data are therefore presented for the entire first study 2008 – 2011 period from Van Zylsrus and for comparison, for the period Dec 2009 – Mar 2011 from KRR station. Data from Van Zylsrus and KRR are presented for the entire current study Sep 2012 – Mar 2015. Note that the KRR weather data are more relevant due to the location of the weather stations at the study site and the confirmed correlation with NDVI data. Cumulative rainfall recorded by the KRR station in the first study was higher than in the current study despite the fact the number of months for which KRR data exist was fewer in the first study. Error bars represent the standard error of rainfall between months and asterisks denote significant difference ($p < 0.003$).

6.4.5. Relation between hot days and rainfall

There was a significant negative relationship between the number of days per month that T_a exceeded 34.5 °C and monthly rainfall, although the slope of the relationship is shallow and there is scatter in the data. The number of days per month that T_a exceeded the hornbill panting threshold temperature decreased slightly with an increase in monthly rainfall (GLM estimate: -0.004 ± 0.002, z = -2.32, p = 0.02) (Figure 7).

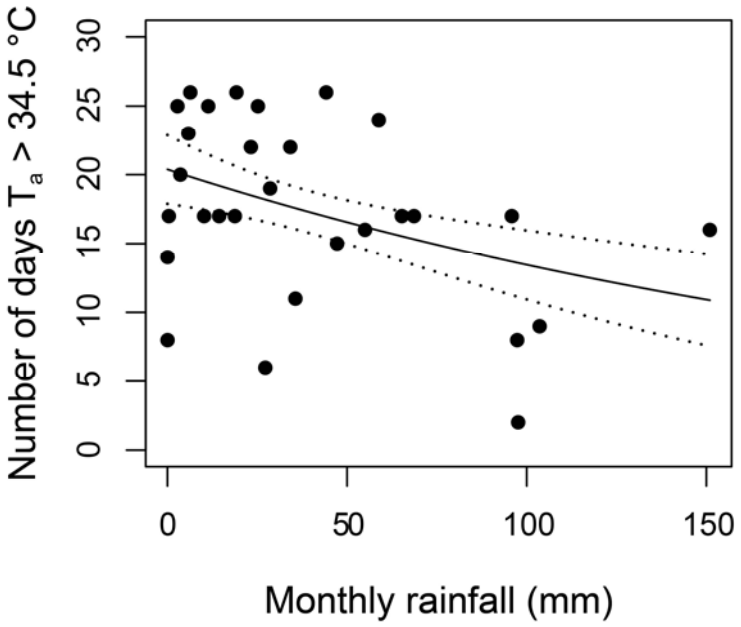

Figure 7 Number of days per month that T_{max} > 34.5 °C as a function of monthly rainfall (mm) at the Kuruman River Reserve. Data were derived from climate data during the Southern Yellow-billed Hornbill nesting period (November to March) of the years 2009 – 2015. The black line represents the predictions of a general linear model with a Poisson error structure and the dashed lines represent the 95 % CI.

6.4.6. Intensity of breeding in the current study

The peak number of nests occupied simultaneously during the current study (2012 - 2015) differed per season, however the peak of breeding occurred during December and January in all three seasons (Season 1: 2012 / 2013; Season 2: 2013 / 2014; Season 3: 2014 / 2015; Figure 8).

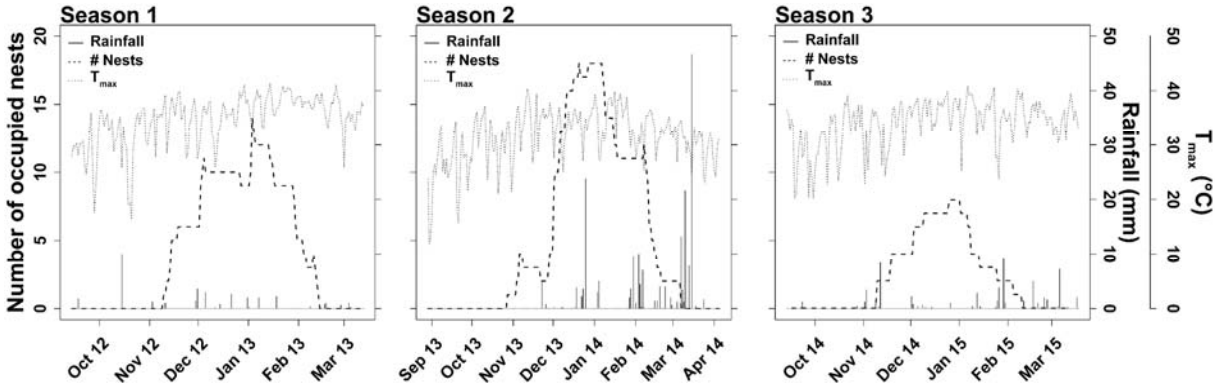

Figure 8 The number of occupied nests, rainfall (mm) and T_{max} (°C) as a function of time of the year (date) during 3 breeding seasons of Southern Yellow-billed Hornbills (Season 1: 2012 / 2013; Season 2: 2013 / 2014; Season 3: 2014 / 2015;). Data are consistent with number of occupied nests given in Table 2.

In the second breeding season, cumulative rainfall was higher, mean T_{max} was lower, breeding initiation was slightly earlier and the last chick of the season fledged later, and the number of occupied nests was higher compared to the first and the third breeding season (Table 2).

Table 2 Cumulative rainfall (mm), mean T_{max} (°C), date of first female nest entry, date of last chick fledged, total number of occupied nests (i.e. number of breeding attempts) and maximum number of nests being occupied simultaneously per Southern Yellow-billed Hornbill breeding season.

Season	Cumulative rainfall (mm)	Mean T_{max} (°C)	First female entry	Last chick fledged	Total of nests occupied	Max. nests occupied
2012 / 2013	36.0 ± SD 0.9	34.7 ± SD 4.6	10-Nov-12	14-Feb-13	17	14
2013 / 2014	196.4 ± SD 4.1	31.6 ± SD 4.8	28-Oct-13	07-Mar-14	18	18
2014 / 2015	62.2 ± SD 1.2	33.9 ± SD 4.4	10-Nov-14	19-Feb-15	8	8

6.4.7. Effect of climatic variables on the total number of breeding attempts per season

The best-fit model for assessing the effects on the total number of breeding attempts contained only rainfall (during the nesting period) and had a model weight of 0.855 (AICc = 60.3, df = 2). No other candidate models were within two ΔAICc points of the top model. The absence of the predictor variable 'pre-breeding rainfall' (two months before the nesting period), suggests that initiation of breeding by the earliest-nesting birds was not triggered by rainfall events in this hornbill population. However, the total number of breeding attempts per season increased with rainfall during the nesting period (GLM estimate: 0.003 ± 0.001, df = 5, z = 3.06, p = 0.002) (Figure 9A), suggesting later-nesting individuals may have used rainfall as a cue. Adding the additional season 2015 / 2016 during which no breeding attempts occurred strengthened this trend slightly (GLM estimate: 0.004 ± 0.001, df = 6, z = 4.79, p < 0.001) (Figure 9B).

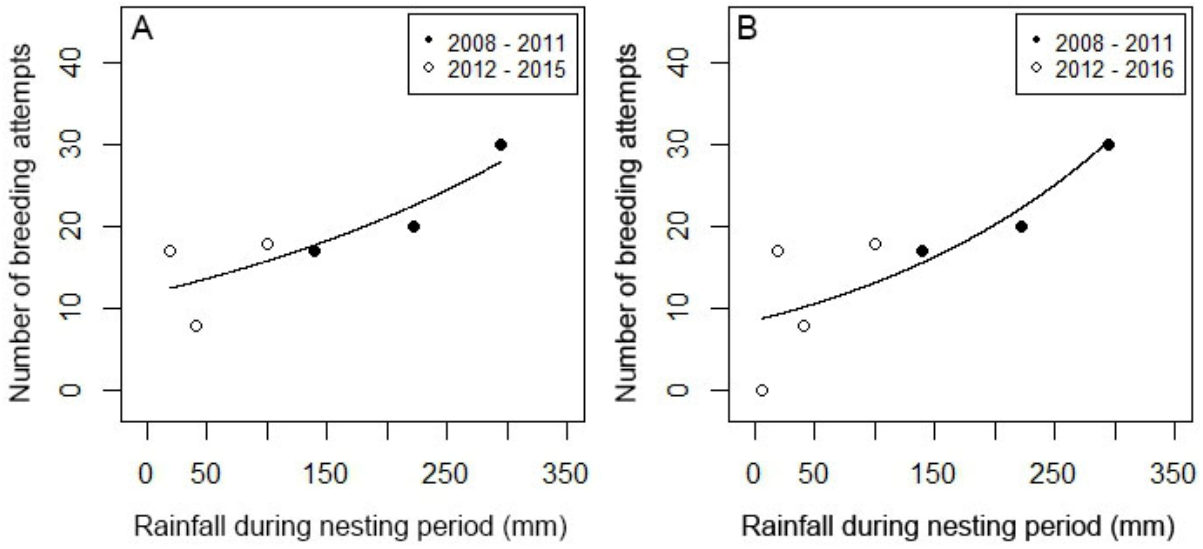

Figure 9 (A) Total number of recorded breeding attempts (Sep - Mar) as a function of rainfall (Sep - Mar) in Southern Yellow-billed Hornbills. Data were derived from 6 breeding seasons. (B) Number of recorded breeding attempts (Sep - Mar) as a function of rainfall (Sep – Mar) in Southern Yellow-billed Hornbills including the hypothesised nesting period of 2015 / 2016 (no breeding attempts). The black line represents the predictions of a general linear model with a Poisson error structure. Data were derived from 7 breeding seasons.

6.4.8. Effect of climatic variables on mean clutch size per season

Mean clutch size was similar across seasons between the 2008 - 2011 study (mean clutch size = 3.8 ± SD 0.4, range 1 - 5) and the current study (mean clutch size = 3.5 ± SD 0.3, range 2 – 5; t = 1.28, p = 0.10). No candidate models were within two ΔAICc points of the null model in explaining variation mean clutch size per season. Variables included in the global model were mean T_{max}, rainfall during nesting period, pre-breeding rainfall, mean T_{max} and rainfall during the winter season.

6.4.9. Female body condition

Female body condition during the period that the females were in the nest with chicks appears to be overall higher during the first study (2008 – 2011) than during the current study (2012 – 2015) (Figure 10), although data from the first study were not available to model this difference statistically. The females in the first study lost on average 18.4 ± 1.3 % of their initial M_b between the period from chick hatch to female nest departure (n = 36) (Finnie, 2012), whereas in the current study, females lost on average 19.3 ± 2.5 % (n = 22; Figure 10). No information is available to compare mass loss of females that successfully fledged chicks versus unsuccessful females. In the current study, female M_b loss was higher for females that successfully fledged chicks 23.9 ± 2.0 % (n = 11) compared to females that failed to fledge chicks 13.7 ± 4.5 % (n = 11).

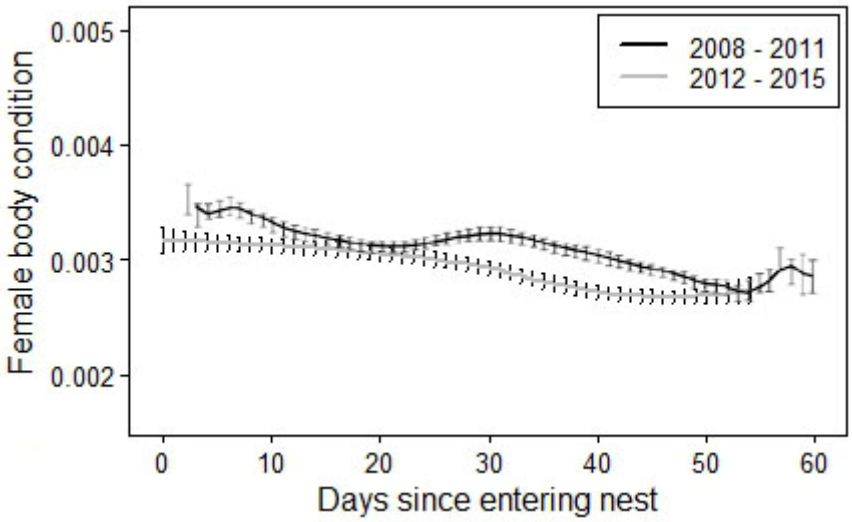

Figure 10 Mean body condition (M_b / tarsus length^3) of female Southern Yellow-billed Hornbills during the nesting period. Data from the first study (2008 – 2011) were derived from 36 females during 41 breeding attempts across two breeding seasons. The black line represents the polynomial regression fit and the error bars represent standard error (data reproduced from Finnie 2012). Data from the current study 2012 – 2015 were derived from 22 females during 38 breeding attempts across three breeding seasons. The grey line represents the polynomial regression fit and the error bars represent standard error.

6.4.10. Reproductive output

Between 2008 and 2011, 58.5 % of recorded breeding attempts resulted in at least one fledgling. By comparison, 42 % of breeding attempts recorded between 2012 and 2015 resulted in at least one fledgling. The proportion of successful nests between 2008 and 2011 was not significantly higher than the proportion of successful nests between 2012 and 2015 (Fisher's exact test: 95 % CI = 0.86 – 4.40, odds ratio = 1.93, p = 0.09). However, average number of fledglings produced per nesting attempt during the first study between 2008 and 2011 was significantly higher than the average number of fledglings per nesting attempt during the current study between 2012 and 2015 (first study: mean 1.03 fledglings, n = 67 nesting attempts; current study: mean 0.49 fledglings, n = 43 nesting attempts; Student's t = 3.11, p < 0.01; Figure 11).

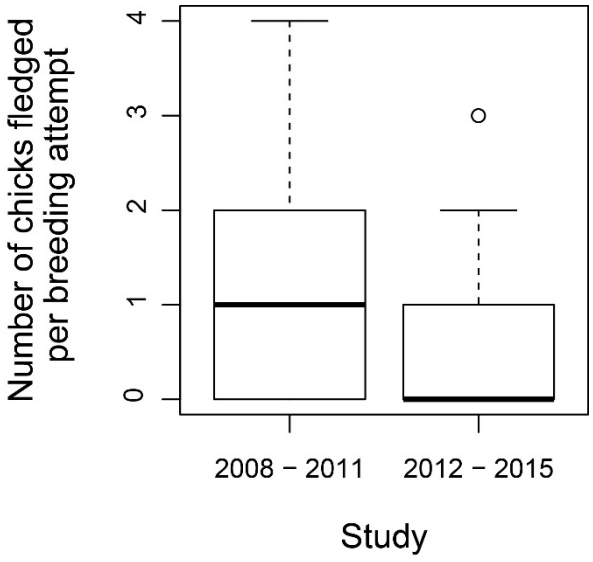

Figure 11 The interquartile range and median of the number of successfully fledged chicks per breeding attempt by Southern Yellow-billed Hornbills. Comparison of the first study, 2008 - 2011 (n = 67 breeding attempts) and the current study, 2012 – 2015 (n = 43 breeding attempts).

6.5 Discussion

Rainfall was associated with the intensity of seasonal breeding attempts by hornbills and furthermore correlated with T_a during the season which had repercussions for the number of successfully fledged chicks per successful breeding attempt. Long term data from the Van Zylsrus weather station confirmed a warming trend in the study region between 1995 and 2015. On average, the number of days per year on which T_a exceeded the hornbill panting threshold temperature increased by 1.8 days annually. This resulted in T_as during the current study (2012 – 2015) being more extreme than during the first study (2008 – 2011). Rainfall was loosely but significantly negatively correlated with the increase in the number of hot days. Rainfall in the current study did not influence the timing of initiation of hornbill breeding as suggested by Finnie (2012) in the first study, but it did impact the number of hornbill pairs that attempted to breed in both studies. Female hornbills in the current study had lower body condition on entry to the nest than females in the first study. Nest success (measured as at least one chick fledged) tended to be lower in the current study ($p = 0.09$) and the number of fledglings per hornbill pair was significantly lower in the current study as compared to the first study (an average of 0.5 chick fledged per nest, versus 1 chick per nest).

The total number of hornbill breeding attempts per season was influenced by rainfall, in keeping with observations of other birds breeding in arid regions (Morrison and Bolger, 2002; Bolger et al., 2005). Cumulative rainfall differed widely by season in the two months prior to nesting. In the first season (2012 / 2013) cumulative rainfall during the two months prior to

nesting was 13 mm, in the second season (2013 / 2014) there was no rainfall prior to nesting and in the third season (2014 / 2015) cumulative rainfall was 7.6 mm during the two months prior to nesting. Despite this, the timing of breeding in the current study was very consistent across all three seasons 2012 / 13, 2013 / 14 and 2014 / 15, with the majority (84 %) of females entering the nest in the beginning of December each season (see Figure 2). Therefore nesting attempts happened largely simultaneously during the breeding season regardless of rainfall patterns. Synchronous breeding of hornbill pairs within one season was also observed in Monteiro's Hornbills (Kemp and Kemp, 1972), Southern Ground Hornbills (*Bucorvus leadbeateri*) (Kemp and Kemp, 1980) and Silvery-cheeked Hornbills (*Bycanistes brevis*) (Moreau, 1936; Moreau and Moreau, 1941).

There are two possible explanations for the synchrony of nesting periods in birds. Seasonality of breeding is mostly observed in birds residing in higher latitudes where long photoperiods stimulate secretion of gonadotropin-releasing hormone and trigger the onset of reproduction (Dawson et al., 2001). Long photoperiods predict food availabily and thus birds should finish breeding before days get shorter. Variation in length of photoperiod in the Kalahari is not as pronounced as in higher latitudes (difference in daylength between summer and winter solstice = 3h37) and might therefore not be a strong breeding stimulus for hornbills. The second possible explanation for hornbills to synchronise breeding is to avoid extra-pair paternity. Due to the capacity of female hornbills for long term sperm storage, one study has hypothesised that there is an opportunity for extra pair paternity in hornbills (Stanback et al., 1998). Finnie (2012) observed female Southern Yellow-billed Hornbills flying off with extra-pair males. The breeding effort by both male and female hornbills is however so great that the benefits of extra-pair copulations (increase of genetic variation / higher genetic quality of extra-pair males) may not outweigh the potential cost if the partner suspects cuckoldry (failed nesting attempt due to female or male nest abandonment) (Stanback et al., 2002). Extra pair paternity was not observed in the study on Monteiro's hornbills by Stanback et al. (2002), suggesting synchronicity of breeding by birds in that study might have been successful in totally preventing it, or that the costs of uncertainty of paternity are too high in this type of breeding system. Synchronised breeding is observed in all of the African hornbills studied to date, with most authors referring to the importance of rainfall to the timing of breeding and its synchrony (Moreau, 1936; Moreau and Moreau, 1941; Kemp and Kemp, 1972, 1980; Finnie, 2012). In the current study, I did not find evidence of rainfall as a trigger for the initiation of breeding in the study population, at least with respect to the earliest-breeding individuals. I propose that rainfall patterns in the Kalahari have altered in recent years and therefore breeding in Southern

Yellow-billed Hornbills is no longer initiated after a notable downpour, but still remains synchronised due to the effects of photoperiod and / or the avoidance of extra-pair paternity.

Female hornbills need to be in good body condition when they enter the nest, as while in the nest they undergo a complete moult, lay and incubate the eggs and rear the chicks. This period of incarceration has a very high energetic demand and females lose about 20 % of their body mass during this period (Finnie 2012 and current study). Initial female M_b is indeed correlated to the probability of nest success (Chapter 4). An extreme example of reduced nesting effort was observed during the 2015 / 2016 season when none of the hornbills in the study population made an attempt to breed. Unfortunately, I was unable to collect M_b of individuals in this season (as our methods for collected M_b data were reliant on birds nesting). However, I speculate that low body condition of birds in the population could have been the reason for the complete absence of breeding at the study site, since rainfall in September and October of that year had been lower than the rainfall recorded in the same periods of this study when hornbills did breed.

Females lost body condition gradually during the time they were incarcerated in the nest, especially after chicks hatched (Chapter 4). In the current study, females left the nest when the mean chick age was 21.6 ± SD 3.3 days and during the period from nest entry to nest exit, females lost 23.9 ± 2.0 % of their initial M_b (data from nests that successfully fledged chicks). The females in the first study stayed in the nest for a similar period until the chicks were 20.3 ± 0.3 days old and lost on average 18.4 ± 1.3 % of their M_b (Finnie, 2012). Since breeding conditions, specifically mean T_{max}, were better (cooler) between 2008 and 2011, I argue that male foraging efficiency and biomass provisioning were likely to have been higher than in the current study (see Chapters 2 and 3 for relationships between T_{max} and male foraging success and provisioning rates). This would lead to females in the 2008 - 2011 study losing less body condition during the nest period and leaving the nest at a higher M_b than the females in the current study. Finnie (2012) concluded that females stay in the nest until the chicks are large enough to compete among each other for food, since females with highly asynchronously-hatched chicks spent more time in the nest than females with more synchronously-hatched chicks. The data presented by Finnie (2012) are based only on successful nesting attempts, as is his conclusion for timing of female departure. However, 20 % of the nests that were unsuccessful in the first study (2008 – 2011) occurred as a result of brood abandonment, cannibalism, and starvation of chicks after female departure. It is likely that these failed nests might have resulted from high T_a during the nesting period (as seen in the current study), although no information was given on T_a during the nesting periods in the 2008 – 2011 study. In Chapter 4 of this study, I concluded that females departed the nest when their M_b reached

a lower limit of ~ 190g regardless of the size chicks had reached at that point. This lower limit existed for both females that successfully fledged chicks and females that failed to fledge chicks. Nesting periods of females that failed to fledge chicks were on average 5 days shorter (16.6 ± 2.7) than nesting periods of females that successfully fledged chicks. This indicates that unsuccessful females lost more mass over a shorter period: due to low initial M_b and high T_a during the nesting period (Chapter 4). My hypothesis that female departure is timed by a lower limit of M_b probably holds for both studies, as it is likely that females who abandoned the nest during the first study (2008 – 2011) did so because of low body condition. Therefore, the female hornbills in this population likely time their departure according to the chicks' fitness when breeding conditions are good and leave the nest in response to their own fitness when breeding conditions are poor: that is, they trade-off the current breeding attempt in favour of potential future breeding attempts (Trivers, 1974).

Clutch sizes were highly uniform between the 2008 - 2011 study (mean clutch size = 3.8) and the current study (mean clutch size = 3.5), irrespective of weather conditions preceding and during breeding, confirming the suggestion by Mills et al. (2005) that Southern Yellow-billed Hornbills invest more effort in egg-laying than Monteiro's Hornbills and have more stable clutch sizes regardless of environmental conditions. One variable likely to have important effects on reproductive output that I was unable to compare between the two studies (2008 - 2011 and 2012 - 2015) was female M_b at the start of the breeding season (intial mass on nest entry) because data on initial female M_b during the 2008 – 2011 study were lacking. Parent birds in good body condition at the beginning of nesting have been found to lay larger clutches early in the season in an arid environment in South Africa (Lloyd, 1999). Large clutches would also be beneficial to confined female hornbills in unpredictable environments, if they could afford to lay them, since it provides them with a food source (both egg and chick) when the males' provisioning efforts are suboptimal.

The number of chicks fledged per successful breeding attempt in the current study was only half of the number of fledglings in the 2008 – 2011 study, despite the similar mean clutch size in both periods. The mortality of chicks (or egg failure) was therefore much higher in the current study. In the current study, recordings of cannibalism of eggs and chicks were not monitored as I did not place cameras within the nest. However, one female was observed consuming her own chick at the time the box was opened for weighing of the female and nestlings, and in a second observation a dead chick that was ejected from the nest was later provisioned back to the nest by the male. Sometimes dead chicks were found in the nest without being eaten by the female or the siblings.

Cannibalism of hornbill chicks has been well studied in the Oriental Pied Hornbill (*Anthracoceros albirostris*) and usually involves the youngest chick of the clutch (Chan et al., 2007; Ng et al., 2011). Hornbill eggs are laid several days apart and since incubation commences with the first egg laid, the chicks hatch asynchronously (Kemp, 1995). In several bird species, notably raptors, larger clutches are laid than the average number of chicks parents can raise. The youngest chicks are regarded as 'insurance' chicks and are kept in case one of the older chicks dies (Wiebe, 1996). Mock and Parker (1986) suggested that 'insurance' chicks have the same reproductive value as their siblings as they can successfully fledge in years of good breeding conditions and they can serve as nutritional value in years with poor breeding conditions. Although the proportion of cannibalised chicks in the current study is unknown, the high mortality rate of chicks is likely to be a result of poor breeding conditions, in which thermal stress and low biomass provisioned may have created energy / water demands in breeding females that promoted cannibalism.

6.6 Conclusions

Weather data confirm that breeding conditions for Southern Yellow-billed Hornbills during the current study were suboptimal in comparison with the study conducted between 2008 and 2011, being characterised by lower rainfall and more variable and extreme T_as. This was reflected by lower numbers of hornbill breeding attempts, more rapid loss of body condition by female hornbills during nesting and lower numbers of successful fledglings per breeding attempt in the current study compared to the 2008 - 2011 study. Although food availability was not quantified in this study, rainfall could influence breeding conditions by increasing prey density prior to and during the nesting period thereby improving foraging opportunity of parent birds. Besides the influence of rainfall on prey density, rainfall is also assumed to lower T_as, although this effect appears to have been quite weak at KRR during the study period. The future climatic scenario for the Kalahari is characterised by increased warming trends and increasingly erratic rainfall (Moise and Hudson, 2008). Poor adult body condition prior to breeding and lack of rain during the breeding season will reduce the number of hornbill pairs attempting to breed. Increases in the number of hot days while the females are in the nest will reduce male provisioning effort (Chapter 3), causing increased egg and chick cannibalism and increasing rates of nest abandonment / early leaving of the nest by females when their M_b reaches a lower tolerable threshold (Chapter 4). The combination of these scenarios under future weather trends can be expected to negatively affect the reproductive success of species discussed above, as well as this population of Southern Yellow-billed Hornbills.

CHAPTER 7 GENERAL DISCUSSION

7.1 Overview

My study extends a growing body of literature on the behavioural mechanisms underlying the vulnerability of species to climate change (Visser et al., 2004; Gaston et al., 2005; Catry et al., 2015; Cunningham et al., 2015; Wiley and Ridley, 2016), showing that behavioural trade-offs for thermoregulation can carry consequences for fitness via sublethal effects on survival and reproductive success. Hornbills are identified as potentially vulnerable to climate change due to their highly energetically demanding breeding system whereby the females are confined to the nest for an extended period of time with eggs and nestlings, and the males are solely responsible for food provisioning (Kemp, 1995). I found that several variables associated with reproductive success, namely provisioning rate, chick growth, parental body mass (M_b), and probability of fledging, are negatively correlated with air temperature (T_a) in a population of desert-dwelling Southern Yellow-billed Hornbills (*Tockus leucomelas*). At a global scale, considerable research on hornbills has focussed on their vulnerability to habitat destruction, international trade, hunting pressure, forest fires, competition for nest cavities and loss of fruiting trees (Poonswad et al., 2005; Kinnaird and O'Brien, 2007; Sodhi and Smith, 2007; Trail, 2007). Little information, however, is available on the impacts of climate change: a particularly important aspect in the Bucerotidae family where parental investment in most species is highly asymmetrical.

In this study, I investigated how hornbill fledging success was affected by weather conditions, by assessing the relationships between T_a, rainfall, parental investment, thermoregulatory behaviours and reproductive performance (Figure 1). I structured this discussion according to the framework for species' vulnerability assessment proposed by Dawson et al. (2011). In this chapter, I discuss the vulnerability of the population of Southern Yellow-billed Hornbills in the Kalahari in terms of their exposure, sensitivity and adaptive capacity as assessed in the previous chapters. I then discuss the implications of my findings at species level, give suggestions for future research and finish with a general conclusion.

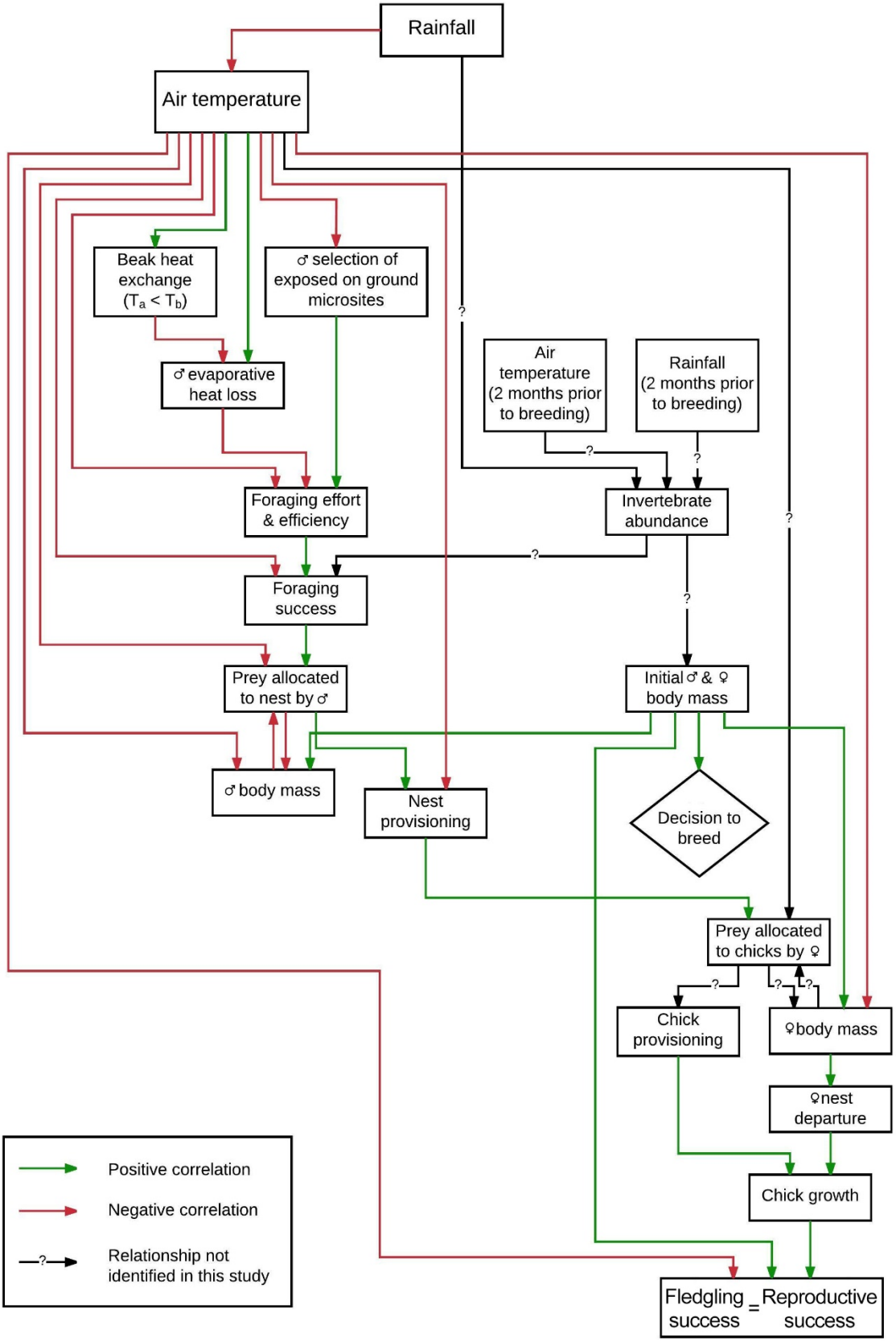

Figure 1 Flowchart indicating the positive (green lines) and negative correlations (red lines) between the variables covered in this thesis. Potential relationships that were not investigated in this study are indicated by question marks (black lines).

7.2 Exposure and sensitivity to the environment

In the most optimistic global warming scenario, temperatures are predicted to increase between 2 °C and 4 °C above pre-industrial levels by the year 2100 and specifically more frequent and longer heat waves and periods of drought are predicted globally (IPCC, 2014). For mammals and birds these predictions suggest an increased pressure on physiological processes supporting homeostasis, and could become fatal if body temperatures are pushed beyond limits (McKechnie and Wolf, 2010; Boyles et al., 2011). Although cases of acute, lethal effects (via dehydration and hyperthermia) of increased temperatures are fairly uncommon, the sublethal, chronic effects (via loss of body condition) of increased temperatures are regularly reported in avian studies (du Plessis et al., 2012; Cunningham et al., 2013c; Edwards et al., 2015; Gardner et al., 2016) as well as in my study. Endotherms are expected to be most vulnerable during periods of excessive energetic demands like reproduction, facing important trade-offs with thermoregulation (Bolger et al., 2005; Dunn and Winkler, 2010; Wong and Candolin, 2015).

At my study site in the southern Kalahari, the number of days on which T_a exceeded 34.5 °C (a temperature threshold above which hornbills face a physiological cost of keeping cool) has increased by 1.8 days annually over the last 20 years (1995 – 2015, Van Zylsrus weather station, SAWS; Figure 6, Chapter 6). Of these hot days, 85.9 % occurred during the hornbill pre-breeding and breeding season (September – March), highlighting the probable additive cost of warming events to an already highly energy-demanding life-history strategy. During the breeding season, male hornbills reduced their exposure to high operative temperatures by moving into shaded sites in trees on hot days, thereby experiencing operative temperatures 10.3 °C below those of exposed sites on the ground (Chapter 2). An increased rate of panting combined with this preference of shaded microsites, however, also reduced their foraging efficiency (Chapter 2) and likely influenced their decision to allocate less prey items to the nest during hot periods (Chapter 3).

In contrast to the males, females were unable to select thermally favourable microsites during hot days as they were confined to the nest and its microclimate. In the current study, 58 % of hornbill breeding attempts failed to produce any fledglings (Chapter 6) and the probability of successfully fledging a chick fell below 50 % when mean T_{max} during the nestling period exceeded 35 °C (Chapter 4). These results confirm that females and chicks in the nest are highly sensitive to increasing T_a. Predicted ongoing climate warming is therefore likely to result in a higher occurrence of female nest abandonment in the future or, if the females are unable to escape the hot nest (due to unfinished moult), higher rates of chick cannibalism or even

female mortality. Hornbills are long-lived birds (Mills et al., 2005) but these changes could conceivably result in decline of the Kalahari Southern Yellow-billed Hornbill population as a consequence of climate change.

7.3 Adaptive capacity to the environment

When looking at the capacity for species to persist into the future under a changing climate, it is important to understand whether phenotypic flexibility in response to hot and / or dry weather events is beneficial in the long term (Wong and Candolin, 2015). The term 'adaptation' is generally associated with evolutionary changes within species (Piersma and Drent, 2003) and current climate change is happening at a faster rate than most species will be able to genetically adapt to (Parmesan, 2006). Therefore, when assessing the adaptive capacity of species in the short-term, research focuses on species' developmental plasticity in response to the current range of climatic variables they experience and whether this plasticity could lead to successful adaptations in the future, or whether behavioural plasticity in fact buffers species against selection pressures that could lead to long-term adaptive genetic change (Piersma and Drent, 2003).

Climatic refugia have been found to be effective in buffering species from exposure to sometimes lethal operative temperatures in extreme habitats (Scheffers et al., 2014). The response of the male hornbills to spend more time in off-ground shaded microsites potentially reduced energy and water spent on heat dissipative behaviour. Behavioural thermoregulation in hornbill males included increasing foraging effort during the cooler times of day and spending more time inactive during hot periods: both behavioural adjustments were likely to reduce the thermoregulatory expense in males on hot days (Chapter 2). These behavioural changes on hot days reduced the pressure of the thermal environment on the males, but had consequences for male foraging success, with knock-on effects for their M_b and the condition of females and chicks in the nest (Chapters 3 and 4). Trade-offs faced by parents between thermoregulatory behaviours, foraging and brood investment may in the long term affect the species' fitness (Cunningham et al., 2015; Edwards et al., 2015).

The body condition of birds prior to breeding is closely correlated with environmental conditions during winter and is likely to influence reproductive performance (Drent and Daan, 1980). In this study, the initial M_b of females at the start of breeding was highly correlated with the probability of nesting success. Females with an initial M_b lower than 220 g had less than 50 % chance of successfully fledging any chicks (Chapter 4). I suggest that female hornbills can assess the quality of the breeding season in terms of environmental conditions via nest box

conditions and the provisioning effort of the males. I observed females abandoning the nest within some days after entering, or staying only until they completed moult (~ 30 days) and then abandoning the nest. In the breeding season of 2015 / 16, none of the hornbill pairs attempted to breed which was likely due to their deficiency in body condition. The previous breeding season 2014 / 15 had a cumulative rainfall of 62.2 ± SD 1.2 mm which was well below the 20-year average of 186.2 ± SD 87.5 mm and no more rain fell during winter. It is likely that prey availability was therefore low and females were unable to regain M_b before the start of the 2015 / 16 breeding season.

Arid zone birds have lower rates of evaporative water loss than birds from more mesic habitats (Tieleman and Williams, 2002a). Still, in this study I found that the evaporative water loss carries the cost of missed foraging opportunity. In Chapter 5, I showed that the large beak functions as a thermal radiator, promoting passive heat loss at T_a s between 30.7 °C and 41.4 °C, likely reducing the costs of evaporative thermoregulation (Chapter 5; van de Ven et al. (2016). The selective pressures that have caused birds to evolve large beaks are still uncertain, but their role in non-evaporative heat loss could have resulted from exposure to high environmental temperatures (Tattersall et al., 2016). I did not quantify evaporative water loss of the hornbills under increasing T_a, but I observed the beak to contribute up to 19 % of the total radiative heat loss. This heat loss mechanism via the beak is therefore likely to be valuable to male hornbills foraging to provide for their entire family. Similarly, I observed females to extrude their beaks through the nest opening at high T_as. I did not measure the specific form of heat loss the females were exploiting here, but it is likely that besides panting the females were exposing the surface of their beak to the air stream outside the nest thereby facilitating non-evaporative heat loss via the beak surface.

7.4 Implications of climate change

The results of this study suggest that this population of Southern Yellow-billed Hornbills is vulnerable to decline as hot weather events increase in frequency, duration and intensity and rainfall becomes less predictable during the southern Kalahari summer. The mechanisms underlying such a decline would be reduced numbers of breeding attempts (Chapter 6), reduced success of these breeding attempts (Chapters 3, 4, 6), and increased rates of mass loss of breeding males (Chapter 3) and females (Chapter 4), with implications for survival especially of incarcerated females undergoing moult in nests. Populations of the same species residing in other regions of southern Africa might not be affected to the same extent by high T_as.

Avian species with large distributions, like hornbills, are often dispersed over a wide range of habitats and environmental conditions. The habitats in the eastern region of the Southern Yellow-billed Hornbill distribution are mesic and are characterised by a higher vegetation density (providing thermal refugia) than the western region of their distribution (Hockey et al., 2005). Same-species individuals from different populations are known to adjust physiological mechanisms accordingly when acclimatised to different environmental factors (Angilletta et al., 2010). Sabat et al. (2006) found that evaporative water losses were lower in a population of Rufous-collared Sparrow (*Zonotrichia capensis*) from an arid site compared to the evaporative water losses of a population from a mesic site. Likewise, mass-specific basal metabolic rates varied among two populations of Southern Red Bishops (*Euplectes orix*) in response to local T_as (van de Ven et al., 2013). The diversity in rates of evaporative water loss and energy expenditure among bird populations can be interpreted as physiological adjustments to match different thermal conditions. These studies show how intra-species variation allows for physiological responses to environmental cues, although it is seldom clear whether these represent local genetic adaptations or phenotypic plasticity. In either case, populations that are exposed to severe changes within their habitat might not have the full suite of genetic variation available to exploit these physiological adjustments optimally (Ghalambor et al., 2007). So even if arid zone populations are likely to have lower adjusted rates of evaporative water loss to save water in desert environments (Smit et al., 2016), climate change might alter T_as beyond thermal tolerances and physiological capacities for evaporative water loss.

In this study, I provide evidence in favour of the idea that sublethal fitness costs could lead to breeding failures and therefore potentially result in population declines. The sublethal fitness costs I observed in this population of Southern Yellow-billed Hornbills were associated with behavioural trade-offs for thermoregulation. Behavioural thermoregulation by organisms has been described as short-term responses to changes in thermal environments (Angilletta et al., 2010; Boyles et al., 2011). Although, possibly beneficial in short-term avoidance of heat, behavioural thermoregulation could reduce fitness of the species in the long term. As evidenced by a study on lizards (*Sceloporus* spp.) which selected cool microsites during hot periods thereby limiting their foraging opportunities, resulting in population declines and even local extinctions (Sinervo et al., 2010). Therefore, the benefit of behavioural thermoregulation to reduce heat loads is dependent on the impact it has on species fitness overall (e.g. missed foraging opportunities) (Cunningham et al., 2015). Sublethal fitness costs associated with behavioural trade-offs for thermoregulation will manifest above certain temperature thresholds. Cunningham et al. (2013b) propose the use of the ‘temperature threshold technique’ as a tool to identify biological meaningful species-specific weather events and demonstrated this by

using examples of two desert birds which experienced reduced foraging success while performing thermoregulatory behaviours. By linking the threshold temperatures to warming trends observed within the species distribution, Cunningham et al. (2013b) were able to identify potential climate refugia for the specific species. In this study, I found that in male hornbills high T_a correlated with heat dissipation behaviour, foraging during cooler periods of the day and preference for shaded sites off the ground. These behavioural trade-offs for thermoregulation resulted in reduced foraging success which had negative impacts on their reproductive success. The sublethal fitness costs observed in this study are likely to result in population declines in the southern Kalahari region within the species' distribution. However, regions of the species' distribution that are less impacted by climatic changes might provide potential climate refugia.

Future weather scenarios predicted for southern Africa anticipate dryer and hotter conditions specifically in the western Kalahari region and much less so in eastern Africa (Moise and Hudson, 2008; Kruger and Sekele, 2012). Southern Yellow-billed Hornbills inhabiting the mesic regions in the east are likely to benefit from higher rainfall, resulting in lower T_as and higher prey densities. Populations of desert-dwelling Southern Yellow-billed Hornbills may face declines in the future as the climate continues to warm, with unknown implications for the ecology of the systems in which they belong. However, this wide-spread species should be more secure in the mesic eastern regions of their distribution where climatic conditions should remain more favourable during the breeding season.

7.5 Future research suggestions

In this study, I present novel findings on the mechanisms linking T_a and reproductive performance in hornbills. My findings also give rise to a new suite of questions that should be the focus of future research aiming to understand the vulnerability of birds to climate change.

The outcomes of this study show that reproductive success in this population of Southern Yellow-billed Hornbills in the arid Kalahari is highly dependent on the mean T_{max} during the nestling period (Chapter 4). I suggest that future research should include a comparison of reproductive success in hornbill populations from arid and mesic habitats. This comparison could give insight whether populations have made behavioural and physiological adjustments to the environments they live in. Specifically, future research should investigate how much phenotypic plasticity currently exists in physiological and behavioural traits among hornbill populations. Translocation experiments of individuals between habitats could reveal phenotypic plasticity in energy expenditure and/or evaporative water loss among populations

in response to climatic variables. I predict that selective pressures associated with desert-dwelling hornbills are expressed differently in populations from higher rainfall areas to the east of their distribution. One possible outcome might reveal that higher humidities in mesic habitats limit the gradient available for efficient evaporative heat loss, thereby negatively affecting hornbill performance in mesic habitats. On the other hand, prey densities and water content of prey are likely to be higher in higher rainfall areas and could lead to higher provisioning rates and higher reproductive success in Southern Yellow-billed Hornbills.

In the current study, I found a strong correlation between female M_b at the start of the nesting season and the probability of nest success (Chapter 4). I predict that nesting success could be higher if hornbills both male and female could manage to achieve higher body condition at the start of the breeding season. Hillstrom (1995) tested reproductive effort in response to initial M_b of male and female Pied Flycatchers (*Ficedula hypoleuca*). They supplied mealworms during incubation and hatching stage and assessed parental M_b changes, clutch size, brood size and fledging success. I propose that a similar experiment should be done in the desert-dwelling hornbills, starting supplementary feeding well before the breeding season to see whether parents with high M_b can invest more in reproduction. Another outcome may be that a temperature threshold may exist above which nesting attempts fail regardless of the body condition of parents, with individuals prioritising their own survival over the current breeding attempt.

During the current study, I aimed to test whether nest boxes with better thermal properties would have a positive effect on nesting success. To assess this, I experimentally insulated some of the nest boxes on the study site. Unfortunately, I did not have enough hornbill pairs breeding in insulated nest boxes and was therefore unable to compare nest outcomes between insulated and uninsulated boxes. Improvement of the thermal properties of the nest could have allowed me to tease apart the effects of male provisioning effort and nest temperature on reproductive success. Since nest box temperatures closely traced T_a during this study (Chapter 4), I propose that this population of hornbills could benefit from breeding in nest boxes that are better insulated against environmental effects of solar radiation and T_a. The orientation of the nest box also influences the thermal properties of the nest and some studies suggest that box orientation can affect reproductive success (Ardia et al., 2006; Butler et al., 2009). If future hornbill research at the study site continues to include factors of nesting success that involves accessing the internal nest, they should improve nest box microclimates and attempt to match these to microclimates recorded in natural cavities. Alternatively, the current nest boxes could be removed from the study site if sufficient natural cavities are available for breeding by

hornbills. Future research could then focus on nesting success of birds breeding in natural cavities.

The results of Chapter 5 suggest that heat exchange capacity of the beak differs not only among species (Toco Toucan (*Ramphastos toco*) versus Southern Yellow-billed Hornbill) but also within species (some hornbills in this study displayed greater rates of heat loss from the beak than others). The efficiency of heat exchange might be associated with beak morphology (e.g. surface area in proportion to the body, keratin thickness) and environmental conditions (e.g. T_a, humidity, rainfall). To test these predictions, I propose future research should focus on the capacity of non-evaporative and evaporative heat exchange in more than one population of Southern Yellow-billed Hornbills from habitats along humidity and temperature gradients. Thermal windows are beneficial because they allow an animal to conserve water that would otherwise be lost via evaporative cooling. In Song Sparrows (*Melospiza melodia*), individuals from water-limited habitats have a larger beak size than individuals of the same species from water-rich habitats (Greenberg et al., 2012). In addition, I hypothesise that large beaks of species residing in humid climates benefit from non-evaporative mechanisms of heat loss because of the low gradient available for evaporative heat loss. Evidence for this is provided by an example from Australia, where parrots from high precipitation areas had larger beak surfaces than the same species of parrots residing in areas with low precipitation (Campbell-Tennant et al., 2015). The association of humidity with beak morphology has also been highlighted in previous studies of Song Sparrows and Yellow Warblers (*Setophaga petechia*) (Greenberg et al., 2012; Luther and Greenberg, 2014). Intra-species comparison should reveal whether humidity or aridity provokes stronger selection for non-evaporative avenues of heat loss.

Opinion of the likelihood of extra-pair parentage in hornbill species in the current literature is still divided, with some studies indicating its potential among hornbills (Stanback et al., 1998; Finnie, 2012) and other studies suggesting non-existence of this behavioural trait (Kemp, 1995; Stanback et al., 2002; Klaassen et al., 2003). In the current study, I suggested that the synchronised timing of nesting could be a strategy to minimise the potential for extra-pair copulations (Chapter 6). On the other hand, this study also confirmed the high cost of reproduction for both males and females and suggested that suspected infidelity could be costly if this resulted in one of the parents abandoning the brood. I propose that further research should focus on the possibility of extra-pair paternity in this study population of hornbills. Methods could include behavioural observations of males and females prior to breeding and males only after the female has settled in the nest, to detect extra-pair activities.

DNA-analysis of collected blood samples could provide evidence of extra-pair activities when existent. If extra-pair parentage does occur in this population, it would raise further questions on how and why this behavioural strategy evolves and persists in populations. Research should then focus on whether the males can detect infidelity of the females and whether this will change their parental effort and the decisions made on food allocation to the nest. This study could reveal whether the extra-parental strategy (gained fitness of improved genetic variation and quality among the brood) is beneficial to females over the potential loss of male parental investment.

Many studies report on the close links between rainfall, vegetation growth and prey densities (Letnic and Dickman, 2005; Pettorelli et al., 2005; Hingrat et al., 2007), however, only little empirical information is available on how trophic structures in desert ecosystems are driven by rainfall (Seely and Louw, 1980; Illera and Díaz, 2006). The reproductive success of Southern Yellow-billed Hornbills in the Kalahari is closely related to changes in prey availability and prey accessibility (in terms of the birds' ability to capture that prey – which is reduced by panting behaviour and seeking of thermal refuges, Chapter 3); correlated to rainfall and T_a. I did not attempt to assess prey availability during this study due to the opportunistic foraging behaviour of hornbills (Kemp, 1995) and difficulty of sampling all types of prey they access. Assessment of prey availability to foraging hornbills would have included a wide variety of sampling methods including pit fall traps, malaise traps and suction traps to count invertebrate abundance (New, 1998) as well as counts of bird and reptile abundance. I suggest that an assessment on seasonal invertebrate abundance in relation to rainfall and T_a in the Kalahari would greatly support our understanding of trophic structures in desert ecosystems, and could potentially provide a reliable proxy of food availability to desert breeding hornbills.

7.6 Conclusions

The current study has produced some novel findings with regards to identifying the mechanisms with which climate change impacts reproductive success in desert birds, using Southern Yellow-billed Hornbills as an example of a potentially highly vulnerable species. Specifically, the effects of high T_as negatively affect reproductive success by increasing the thermoregulatory costs to the males, the females and the offspring, as shown by the direct links between T_a, foraging success, provisioning rates, and diurnal M_b changes. Most ecological studies on bird species potentially vulnerable to climate change do not contemplate the risk of extinction (Şekercioğlu et al., 2012). This suggests that more studies should focus on species' physiological tolerances, behavioural thermoregulatory strategies, and the potential fitness consequences of trade-offs between these, in combination with local climatic

conditions in order to predict future scenarios for species under climate change (Khaliq et al., 2014). All hornbill species, except two species in the genus *Bucorvus*, employ the high-energy demanding breeding strategy whereby the females are confined to the nest cavity and the males are solely responsible for food provisioning (Kemp, 1995). I predict that besides the known impacts of habitat destruction, international trade, hunting pressure, forest fires, etc., climate change is an additional threat affecting persistence of hornbill populations globally. My comparison of Southern Yellow-billed Hornbill reproductive success over a period of seven years (2008 – 2011; previous study by Finnie (2012) and 2012 – 2015; current study, Chapter 6) showed that reproductive success in this population has already declined over this relatively short time scale in response to changing weather conditions. Currently, no conservation efforts for the Southern Yellow-billed Hornbills are in place since the species' status given by IUCN is 'least concern' (IUCN, 2011). Southern Yellow-billed Hornbills are relatively long-lived (~ 23 years, Strehlow, 2001) and it seems likely that the frequency of suboptimal breeding seasons will determine the number of successful fledglings produced within a hornbill lifetime. The population of Southern Yellow-billed Hornbills in the southern Kalahari is currently under stress during hot weather events. If the trend of high T_as and unpredictable rainfall continues, and individuals face an increased frequency of poor breeding seasons during their lifetimes as a consequence, this population is likely to come under pressure. This study contributes to the understanding of chronic sublethal fitness costs mediated via behavioural thermoregulatory trade-offs. In addition, this study reiterates the ecological implications of climate change applicable to numerous species.

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